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LAND BRIDGES AND ECOLOGY IN BAT DISTRIBUTION ON ISLANDS OFF THE NORTHERN COAST OF SOUTH AMERICA

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INTRODUCTION

The zoogeography of insular faunas has always posed special problems. Prominent among these is the question of faunal composition. Whether an island is of the continental or of the oceanic type, its fauna usually differs significantly from that of nearby mainland areas. This phenomenon, in any given case, appears to be determined by two main factors.

The first of these, which has received the most attention, is the past history of the island in terms of former land connections, or, if these have been absent, of ease of overwater dispersal. This latter factor may involve either absolute distance from the mainland or the presence or absence of special aids to overwater transport. Under the last heading would be classed favorable hurricane paths and large rivers which could propel natural rafts to the island in question.

The second factor is the ecology, past and present, of the island and of the mainland source from which the insular fauna must come. It is evident that unless the ecologies of two islands are at least approximately similar, a faunal comparison is not likely to elucidate the means by which they were colonized. Under these circumstances it is often very difficult to determine whether the water barrier as such or the ecological difference has prevented certain forms from colonizing the island.

For some time I have been much concerned about the relative roles of these two major factors as applied to the West Indian mammal fauna, particularly as they concern its largest component, the order Chiroptera. The general consensus, with which I am in hearty agreement, is that the entire mammal fauna has reached these islands across water (Simpson, 1956). It is also clear that the bat fauna represents, on the whole, an accumulation of invaders which have reached the Antilles at various times. This is shown by the extremely uneven degree of differentiation shown by the various species and higher groups. At one extreme there is an endemic subfamily, the Phyllonycterinae, while at the other, some West Indian bats are indistinguishable from their mainland representatives. An interesting feature is that

the better differentiated forms, presumably the earlier invaders, are relatively few in number, whereas the undifferentiated or weakly differentiated species form a decided majority. This implies that either colonization has become progressively easier with time or more likely there has been continual replacement of older colonizers by more recent invaders with roughly similar ecological preferences so that few of the earlier immigrants, these being now well differentiated, persist.

The problem of whether relative ease of dispersal or ecological factors are most important in determining establishment of species on islands was to some extent discussed by Koopman and Williams (1951). One avenue of attack would seem to be a study of the bats occurring on the islands off the northern coast of South America, some of which closely adjoin or even are included in the West Indies, and which differ considerably among themselves both in ecology and former land connections.

The Coastal Islands of Northern South America

The islands under consideration all lie fairly close (within 100 miles) to the Venezuelan coast between the Guajira peninsula on the west and the Orinoco delta on the east. The western (Dutch) and central (Venezuelan) islands of this group have been treated geographically, ecologically, and faunistically by Hummelinck (1940). Of the three eastern (British) islands, Grenada is generally included in the West Indies, whereas Trinidad and Tobago, both lying on the continental shelf, form part of the Brazilian subregion of zoogeographers. Virtually the only islands of the group on which bat collections appear to have been made are Aruba, Curacao, Bonaire, Margarita, Trinidad, Tobago, and Grenada. Further discussion will be concerned almost exclusively with these seven islands. Inspection of any map showing the depth of the water around these islands shows that the channels separating the islands from the mainland and from one another are all either quite shallow (less than 300 feet) or relatively deep (more than 700 feet). Since the oscillations of sea level during the Pleistocene are generally considered to have reached some point between 350 and 400 feet below the present sea level (Flint, 1947), it seems fairly safe to assume that the shallow channels were dry land, but that the deep

Fig. 1. Map of the islands off the coast of South America discussed in this paper. The broken line marks the 100-fathom line separating continental from oceanic islands.

ones remained water gaps during the Pleistocene glaciations. On this assumption, Aruba, Margarita, Trinidad, and Tobago should be considered continental, whereas Curacao, Bonaire, and Grenada would be oceanic in a broad sense (see fig. 1). Although Voous (1957) finds that a considerable portion of the Aruba bird fauna is of West Indian origin and is therefore inclined to consider this island to have had a long separation from the mainland, the shallow water separating it from the mainland to the southwest would appear to make its Pleistocene glacial connection with the mainland inevitable.

Ecological classification is more difficult since the feature which is most important is an estimate of ecological diversity. In the absence of personal acquaintance with the islands in question, the two best measures would appear to be general vegetation types and size of the island (with which maximum elevation is fairly well correlated). On the first point, the major distinction would appear to be whether there is any rain forest or whether the entire vegetation is of a scrubby xerophytic type. From the account of Hummelinck (1940), Aruba, Curacao, and Bonaire appear to be essentially of the xerophytic type, but Margarita does have in places a more lush vegetation which approaches rain forest conditions. Trinidad, Tobago, and Grenada have, at least in the mountains, a rain forest, at least of the montane type (Beard, 1949).

In order of size, Trinidad is by far the largest, then Margarita, Curacao third in size, while the other four are relatively small. Ecologically then, Trinidad would appear to be the richest, Tobago and Grenada probably next, then Margarita, while the three Dutch islands, especially Aruba and Bonaire, are certainly the poorest. (These points are summarized in table 1 and figure 2).

Sources of Information on the Bat Fauna

This study was prompted by the receipt by the American Museum of Natural History of two collections of bats from the islands in question, both of which included new records. The first, from the three Dutch islands, was made by Mr. E. McGuire of the American Museum of Natural History. The second was a Beebe collection from the Arima valley in Trinidad. These, together with

Table 1. *Classification of the islands off the northern coast of South America*

1a	Continental islands	2a	With rain forest
	Trinidad		Trinidad
	Tobago		Tobago
	Margarita		Grenada
	Aruba	2b	Traces of rain forest
1b	Oceanic islands		Margarita
	Grenada	2c	Xerophytic vegetation
	Curacao		Aruba
	Bonaire		Curacao
			Bonaire
3	Rank in order of size	4	Rank in order of maximum elevation
	Trinidad—1864 sq. mi.		Margarita—3241 ft.
	Margarita—846 sq. mi.		Trinidad—3085 ft.
	Curacao—403 sq. mi.		Grenada—2749 ft.
	Grenada—133 sq. mi.		Tobago—1891 ft.
	Tobago—116 sq. mi.		Curacao—1120 ft.
	Bonaire—112 sq. mi.		Bonaire—787 ft.
	Aruba—70 sq. mi.		Aruba—617 ft.

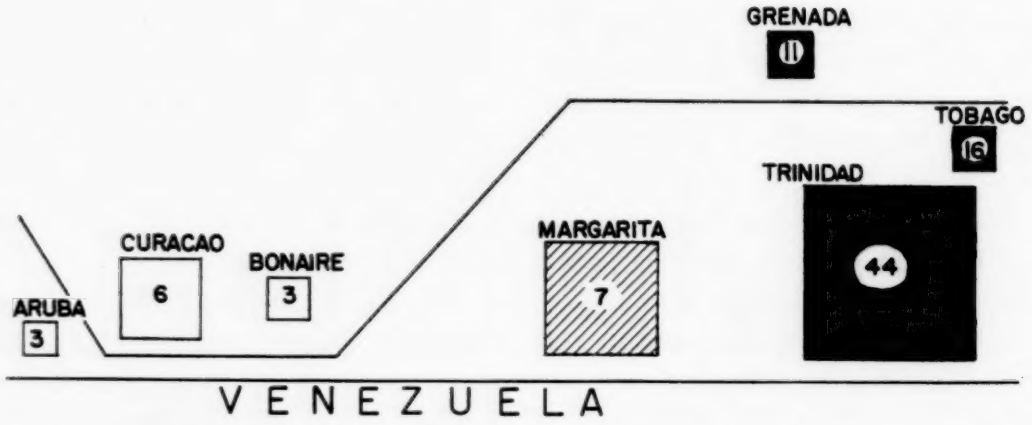

FIG. 2. Diagrammatic comparison of the islands indicated in figure 1. The size of each square is proportional to the size of the indicated island. The shading of each square indicates the vegetation type of the island (black—rain forest, diagonal lines—traces of rain forest, white —xerophytic vegetation only). The numbers refer to the number of bat species recorded from the island, taken from table 2. (Recently published records increase the number for Trinidad to 53.) The straight line near the bottom represents the Venezuelan coastline, the zigzag line above it the 100-fathom line.

study of Trinidad, Tobago, Grenada, and Margarita bats in various museum collections, particularly the American Museum of Natural History, Museum of Comparative Zoology, and United States National Museum, have been the chief

TABLE 2. *Distribution of bats on islands off the northern coast of South America*

Species	Aruba	Curacao	Bonaire	Margarita	Trinidad	Tobago	Grenada
Rhynchiscus naso					S7		
Saccopteryx bilineata					S7		
Saccopteryx leptura					S7	J	
Peropteryx macrotis (1)				Hu	D	MC	J
Diclidurus albus					V-F		
Noctilio leporinus					D		J
Chilonycteris personata					G		
Chilonycteris parnellii (2)				Hu	D		
Pteronotus davyi					G		J
Mormoops megalophylla (3)	Hu	Hu		Hu	V-F		
M. (Micronycteris) megalotis (4)				Hu	D	J	U
M. (Micronycteris) minuta					G		
M. (Xenoctenes) hirsuta					G		
M. (Lampronycteris) platyceps					S9		
M. (Trinycteris) nicefori					G		
Lonchorhina aurita					G		
Tonatia venezuelae					S1		
Anthorhina crenulata					G		
Phyllostomus discolor					D		
Phyllostomus hastatus (5)					D	MC	
Trachops cirrhosis					G		
Vampyrum spectrum					S1		
Glossophaga soricina (6)					D		
Glossophaga longirostris (7)	A	A	A	MC		Hs	J
Choeroniscus intermedia					G		
Anoura geoffroyi					G		
Leptonycteris curasoae	Hu	Hu					
Carollia perspicillata (8)					D	Hs	A1
Sturnira lilium					G		
Vampyrops helleri (9)					S5		
Vampyrodes caraccioli					S1	Hs	

TABLE 2.—*Continued*

Species	Aruba	Curacao	Bonaire	Margarita	Trinidad	Tobago	Grenada
Uroderma bilobatum					G		
Chiroderma villosa					G	J	
Enchisthenes harti					G		
Artibeus jamaicensis (10)					D	J	J
Artibeus lituratus (11)					D	J	J
Artibeus cinereus (12)					G	Hs	MC
Centurio senex					G	J	
Diaemus youngi					G		
Desmodus rotundus					D		
Natalus stramineus					S1		
Natalus tumidirostris		K					
Thyroptera tricolor					G		
Furipterus horrens					G		
Myotis nigricans		Hu	K		D	J	M+A
Myotis argentatus (13)					A		
Pipistrellus subflavus (14)					A		
Eptesicus brasiliensis (15)						MC	
Rhogeesa parvula (16)				Hu	Ha		
Lasiurus borealis					G		
Dasypterus ega					G		
Promops centralis					D		
Molossus rufus					G		
Molossus major (17)		Hu	Hu	Hu	D	J	J
[*Tadarida brasiliensis*] (18)						U	
Total	3	6	3	7	50	16	11

Explanation of symbols: A (American Museum of Natural History specimens); Al (Allen, 1911); D (Dalquest, 1951); G (Greenhall, 1956); Ha (Hayman, 1938); Hs (Husson, 1954); Hu (Hummelinck, 1940); J (Jones, 1951); K (Koopman, 1958); M+A (Miller and Allen, 1928); MC (Museum of Comparative Zoology specimens); S1 (Sanborn, 1941); S5 (Sanborn, 1955); S7 (Sanborn, 1937); S9 (Sanborn, 1949); U (United States National Museum specimens); V-F (Vesey-Fitzgerald, 1936).

sources of first-hand information on the bats of the islands in question.

Several important papers have appeared during the last 25 years on the bats of these islands. These include Hummelinck (1940) on the Dutch islands and Margarita; Vesey-Fitzgerald (1936), Sanborn (1941), Hayman (1938), Dalquest (1951), and Greenhall (1956) on Trinidad; Jones (1951) and Husson (1954) on Tobago, the former also on Grenada. From these sources, both published and unpublished, and from a few earlier publications, a list (table 2) can be prepared which probably includes the great majority of the species which occur on these islands. Discussion of certain new records and taxonomic questions which have emerged from this study are given in the Appendix.

DISCUSSION

Of the 55 species listed in table 2 (with one exception apparently all of direct South American origin), Trinidad with 50 has by far the greatest number. This is to be expected since it is the only island that combines continental position, large size, and presence of rain forest. Tobago comes next with 16 species. While the true number is probably larger (Tobago having been less adequately collected than Trinidad), it seems clear that the smaller size and more peripheral position of Tobago, together perhaps with its lower elevation, has permitted it to receive and maintain a much smaller number of species. Grenada with 11 species

is third. Here small size is combined with deep-water separation and therefore its poorer bat fauna, in comparison with Tobago, indicates the effectiveness of a rather narrow but permanent water gap, especially noteworthy in view of Grenada's greater elevation. It is interesting to note that all three islands with definite rain forest, even though small and oceanic, as is Grenada, are well ahead of any of the other islands. Next in rank, with seven species, is Margarita, which is continental, rather large, and has traces of rain forest. It is possible that here too, more collecting will increase the known number of species considerably. The three dry western islands all have very poor bat faunas. Even here, Curacao, oceanic but the largest and highest, has the greatest number of species, while Aruba, small and continental, has no more than Bonaire, small and oceanic. These points are summarized in figure 2.

I have not done much tabulation of number of species in nearby mainland areas, chiefly because of the difficulty in finding relatively small mainland areas in which good bat collections have been made. Two such areas have been worked out, both unfortunately, considerably larger than any of the offshore islands under discussion. This is probably more than made up, however, by the virtual certainty that the list for each area is far from complete. The first region is a fairly restricted area in northern Colombia (Hershkovitz, 1949) from which 45 species of bats have been recorded. The second region is a fairly narrow strip along the coast of northern Venezuela from about longitude 67°W to 69°W (J. A. Allen, 1911; Robinson and Lyon, 1902; Tate, 1947) from which records of 34 species have been obtained. The relatively poor showing of these two mainland areas compared with Trinidad is probably a measure of the less adequate bat collecting on the mainland.

Another interesting comparison is between the bat and Passerine bird faunas of the seven islands in question. On the basis of several sources (Bond, 1956; Hellmayr, 1924–1938; Voous, 1957; Yepez, Benedetti, and Phelps, 1940 being most important), the following numbers of species of Passeriformes have been drawn up: Trinidad 109, Tobago 41, Margarita 36, Grenada 23, Curacao 14, Aruba 13, Bonaire 13. In general these figures parallel those for the bats, the principal differences being the much better showing of Margarita, Aruba, and Bonaire as far as the bird figures are concerned. This may simply indicate bat collecting on these three islands or it may reflect certain ecological discrepancies between bats and Passerine birds, such as the non-existence of seed- or worm-eating bats or of blood-lapping birds.

It is clear, therefore, that the number of bat species on a given island correlates much better with the ecological rank of the island than with the presence or absence of former land connections. Thus it appears that ecology has been the major factor determining the number of species which have become established on the various islands. Generalizing, it would seem that the element of ecological difference must always be taken into account when considering the probable former history of islands on the basis of their fauna.

One could argue, however, that these islands off the northern coast of South America represent a special case. The water barriers, however permanent, are relatively narrow and may not be very serious obstacles to flying forms such as bats. The ecological differences among the various islands, on the other hand, are rather extreme and it might therefore be expected that ecology would play the dominant role. Hence, it would seem profitable to consider a group of islands separated from the mainland by wider water barriers, but which present ecological opportunities roughly comparable with those of adjacent mainland areas.

Such a group of islands is to be found

in the Greater Antilles. The four large islands (Cuba, Jamaica, Hispaniola, Puerto Rico) are separated from the mainland and from one another by relatively broad and deep sea barriers. Ecologically they are large and high enough to exhibit a degree of ecological diversity roughly comparable with nearby continental areas. Under these conditions, one might expect that the presence and width of the water barriers would dominate the situation and that ecology would play a relatively minor role.

At first sight, the Greater Antillean bat faunas seem to bear this out, since they are markedly poorer than those of adjacent continental insular and peninsular areas. If we count only species known to be represented by living populations, the figures are as follows: Cuba 23, Jamaica 20, Hispaniola 16, Puerto Rico 12. This compares with 50 species from Trinidad given in this paper and 32 species for Yucatan (see Hatt, 1953). It may also be noted that the two Greater Antillean islands closest to the mainland (Cuba and Jamaica) have the richest bat fauna, whereas Hispaniola, larger and higher than Jamaica and probably the richest of the four ecologically, has a poorer bat fauna in agreement with its more peripheral position necessitating at least two overwater colonizations. Finally, Puerto Rico, the most peripheral (and it must be admitted the poorest ecologically), has the poorest bat fauna.

Closer inspection, however, reveals that the picture is not as simple as it appears at first sight. Fossil evidence presented in previous papers (Koopman and Williams, 1951; Williams, 1952), summarized with additions and corrections in table 3, indicates that even in the relatively short time since the late Pleistocene there has been some replacement among the bats, at least in Jamaica, certain forms becoming extinct, others coming in more recently to take their places. The importance of this factor is shown by the fact that relatively few of the

TABLE 3. *Records of Jamaican bat genera and subgenera (dubious records and accidentals omitted)*

	Fossil	Surface and subsurface	Collected in the flesh
Noctilio		+	+
Chilonycteris	+	+	+
Mormoops	+		+
Macrotus	+	+	+
Tonatia	+		
Glossophaga		+	+
Monophyllus	+	+	+
Brachyphylla	+		
Artibeus		+	+
Ariteus	+	+	+
Erophylla	+	+	+
Reithronycteris	+	+	+
Natalus	+		+
Chilonatalus			+
Eptesicus	+		+
Lasiurus			+
Tadarida		+	+
Eumops		+	+
Molossus		+	+

Greater Antillean bats are very different from mainland relatives and most appear to be so poorly differentiated that invasion of the Greater Antilles prior to the Pleistocene appears to be most unlikely. Since the Greater Antilles have probably been available for bat colonization ever since the Miocene, this implies either that the rate of colonization until recently was unusually slow or else that most of the earlier colonists have since been replaced by later invaders. Of these two alternatives, the latter appears to be by far the most probable and is apparently of rather frequent occurrence on oceanic islands (see Mayr, 1940).

It is, however, difficult to reconcile the concept of replacement with the evidence that the bat fauna is poorer than would be expected on the basis of the ecology. The relatively poor bat fauna strongly suggests that there are numerous unfilled ecological niches, but if the number of past invasions has been much greater than the number of species now living, one would expect that all ecological niches would long ago have been filled. This

apparent paradox can be explained, however, if we assume that ecological conditions in the Greater Antilles have been constantly changing, with old ecological niches disappearing and new ones opening up. In mainland areas, such changes need not result in the impoverishment of the fauna since species already adapted to the new conditions will usually be present in adjoining areas and can move in without delay. An effective water barrier, however, might delay this process for a considerable length of time with the result that at any given time level, unoccupied ecological niches would be present. This would explain the small number of species present on islands such as the Greater Antilles that are relatively rich ecologically. The effect would, of course, be particularly pronounced immediately after a period of great climatic changes such as the Pleistocene. Islands such as Hispaniola, where unfilled ecological niches would probably only be occupied after crossings of two water barriers had taken place, would be expected to show this phenomenon to an unusually marked degree.

It therefore appears that the poorer bat faunas of the Greater Antilles as compared with nearby comparable continental areas such as Trinidad or Yucatan are not due to the presence of the water gaps alone as is often supposed. Neither is it so much a function of ecology as was suggested by Koopman and Williams (1951). Rather it appears to result from an interaction of the two factors.

Summary

The relative roles of geographical barriers and ecology in determining the faunal composition of islands is discussed in relation to the bats of certain islands off the northern coast of South America. A complete list of the bats of these islands is given, largely compiled from the literature, but also including some new records. On these islands ecological differences play a much more important role than does the presence of permanent water gaps in determining the number of species a given island supports. The applications of these findings to the somewhat different problems encountered in the Greater Antilles is discussed and a hypothesis involving interaction of water barriers and ecology is presented to explain certain characteristics of the West Indian bat fauna.

Acknowledgments

I am chiefly indebted to the Mammal Department of the American Museum of Natural History which made available the two important collections mentioned here as well as the general facilities of the department, particularly to Mr. E. McGuire who gave me the benefit of his first hand experience in the Dutch islands. I am also happy to acknowledge the help of the Mammal Departments of the Museum of Comparative Zoology at Harvard University, the United States National Museum, and the Chicago Natural History Museum for their facilities, including, in the case of the latter institution, loan of comparative material. I also wish to thank Drs. Ernest Williams and Ernst Mayr of Harvard University, Dr. Paul Martin of the University of Montreal, and Drs. Max K. Hecht and Daniel Marien of Queens College, Flushing, N. Y., for critical suggestions in regard to the manuscript. The map was prepared by Mr. John J. Fagan of the Department of Geology, Colombia University.

Appendix—New Records and Taxonomic Problems

In the distributional table (table 2) and in the following taxonomic remarks, the species are considered the units and subspecies are largely ignored. This is done for two reasons. First, it is believed that the distribution of separate subspecies is much less significant than that of each species as a whole, particularly in a study such as this. Secondly because subspecific identification is much more difficult than is identification of species and hence there is much greater chance for misidentifica-

tion, especially in what is largely a compilation, such as the present work. The numbers after certain species refer to the taxonomic notes below.

1. *Peropteryx macrotis.* This name is used for the species by Dalquest (1951) in Trinidad and Jones (1951) in Grenada. Hummelinck (1940) uses the name *P. canina trinitatis* for the Margarita record, but this is considered a specific synonym of *P. macrotis* by Sanborn (1937). The Museum of Comparative Zoology has five specimens (MCZ 16616–16620) from Tobago.

2. *Chilonycteris parnellii.* Most writers have recognized two species of large *Chilonycteris,* a mainland (*C. rubiginosa*) and a West Indian (*C. parnellii*). I have elsewhere (Koopman, 1946; Koopman and Martin, 1958) given my reasons for considering both to be conspecific under the name *C. parnellii.* Both Dalquest (1951) and Hummelinck (1950) record large *Chilonycteris* from the islands under consideration. Dalquest (1951) identifies the Trinidad population as *C. rubiginosa,* whereas Hummelinck calls the form on Margarita *C. parnellii.* While it is not clear whether Hummelinck uses this name in the broad or the narrow sense, it seems reasonably certain that his identification is correct as to species.

3. *Mormoops megalophylla.* Vesey-Fitzgerald (1956) lists this species from Trinidad, although Miller (1902) had previously described the Trinidad *Mormoops* as *M. tumidiceps.* Hummelinck (1940) lists *M. m. megalophylla* from Margarita, *M. m. intermedia* from Aruba and Curacao. Comparison of a single Trinidad individual and series from Aruba and Curacao (mostly collected by McGuire) with mainland specimens, particularly with a good series from Guatemala, convinces me that both *intermedia* and *tumidiceps* are best considered subspecies of *M. megalophylla,* since the differences are hardly greater than those between *M. m. megalophylla* and *M. m. senicula* on the mainland and are certainly much less than between any of these forms and the West Indian *M. blainvillii.* Aruba specimens seem to be more or less intermediate between *M. m. megalophylla* of the mainland and *M. m. intermedia* of Curacao.

4. *M. (Micronycteris) megalotis.* The United States National Museum has a single specimen from Grenada (USNM267846). It is, of course, impossible to say whether this represents a single accidental record or whether there is a population on Grenada. The species has also been recorded from Tobago (Jones, 1951), Trinidad (Dalquest, 1951) and Margarita (Hummelinck, 1940).

5. *Phyllostomus hastatus.*—Dalquest (1951) records this species from Trinidad and the Museum of Comparative Zoology has a specimen from Tobago (MCZ11262).

6. *Glossophaga soricina.* As noted below, this species is confused with the next by Hummelinck (1940), probably because they are very similar externally and are somewhat difficult to distinguish unless the skulls are removed and cleaned. The only island under consideration, therefore, where *G. soricina* is actually known to occur is Trinidad, from which it was recorded by Dalquest (1951).

7. *Glossophaga longirostris.* Hummelinck (1940) records *G. soricina* from the three Dutch islands, but material collected by McGuire from Aruba, Curacao, and Bonaire (AMNH149399–14904) seems all to pertain to *G. elongata,* described by Miller (1900) from Curacao, but tentatively synonymized with *G. soricina* by Hummelinck. While in full agreement with Miller (1913) that *G. soricina* and *G. longirostris* are distinct sympatric species on the South American mainland, I feel that on the basis of the material I have seen, the allopatric *G. elongata* is much less distinct and is best considered a subspecies of *G. longirostris.* Hummelinck's record of *G. soricina* from Margarita is taken from G. M. Allen (1902). I have examined the specimens in question (MCZ8541–8543) and while they are not adequate for subspecific determination, they seem clearly to belong to *G. longirostris* rather than to *G. soricina.* Hummelinck (1940) also records *G. soricina* from the Testigos (very small islands on the continental shelf northeast of Margarita), but the status of this population is not too clear. It is most unlikely, however, that these specimens are really *G. soricina,* since the Testigos individuals are said to have larger ears than the *Glossophaga* from the three Dutch islands. Comparison of alcoholic specimens of *G. l. elongata* from all three islands with *G. soricina,* however, reveals that the latter have the shortest ears. It is therefore probable that the Testigos population belongs to *G. longirostris,* perhaps representing an undescribed race. *G. longirostris* has also been recorded from Patos island in the channel between Venezuela and Trinidad (Sanborn, 1941), while Husson (1954) has recorded it from Tobago and Jones (1951) from Grenada.

8. *Carollia perspicillata.* G. M. Allen (1911) recorded this species from Grenada as *Hemiderma perspicillatum. Carollia* is now considered the correct name for the genus. The species has also been recorded from Tobago (Husson, 1954) and Trinidad (Dalquest, 1951).

9. *Vampyrops helleri.* A single specimen from Trinidad in the Beebe collection was mentioned by Sanborn (1955).

10. *Artibeus jamaicensis.* This species was

recorded from Tobago and Grenada by Jones (1951) under the name *A. planirostris*. As mentioned by Dalquest (1951), who records it from Trinidad, this species, with its subspecies *trinitatis* and *grenadensis*, is conspecific with *A. jamaicensis*.

11. *Artibeus lituratus*. As Hershkovitz (1949) has shown, *A. lituratus* and its subspecies *palmarum* are specifically distinct from *A. jamaicensis*, with which they are associated by Jones (1951), who recorded the species from Tobago and Grenada. Dalquest (1951) has recorded the species from Trinidad.

12. *Artibeus cinereus*. This species was recorded from Trinidad by Greenhall (1956) and by Husson (1954) from Tobago. The Museum of Comparative Zoology has a single specimen (MCZ14599) from Grenada. In the latter case, as with Grenada *Micronycteris*, it it possible that this is an accidental record.

13. *Myotis argentatus*. Five specimens (AMNH149588–149591, 149593) collected by Beebe in Trinidad agree with the diagnosis and figures of *M. argentatus* given by Dalquest and Hall (1947) and disagree with specimens of *M. albescens* from Ecuador and Paraguay as well as with the diagnoses of all other South American *Myotis* species given in Miller and Allen (1928). In spite of the great distance from Veracruz, the only place from which *M. argentatus* had previously been recorded, this identification seems the most reasonable one at the present time.

14. *Pipistrellus subflavus*. A single individual (AMNH149592) collected by Beebe in Trinidad agrees with this species in size, dental formula, ear form, and the various specific characters listed by Hall and Dalquest (1950). This record represents a considerable extension in the range of this North American species south from Honduras.

15. *Eptesicus brasiliensis*. The Museum of Comparative Zoology has a single *Eptesicus* from Tobago (MCZ11267) identified as *E. hilarii* with a forearm length of 40 mm. According to Shamel's (1940) arrangement, it therefore belongs to the *E. brasiliensis* group. Unfortunately the taxonomy of this group appears to be badly confused. Shamel lists 10 species in the group from South America east of the Andes, but Thomas in an earlier (1920), though more critical, paper recognized only 8, *hilarii* being considered a synonym of *E. brasiliensis* and *auripendulus* evidently being considered unidentifiable, as Shamel suggests. Excluding now the forms from well south of the Amazon, we are left with only *brasiliensis, melanopterus, andinus,* and *chapmani*. Of these, *andinus* has been made a subspecies of *E. brasiliensis* by Hershkovitz (1949), while *chapmani* is considered a subspecies of *propinquus* by Goodwin (1953), *propinquus* also being considered a subspecies of *brasiliensis* by Hershkovitz. It thus appears that only two species are under consideration, *E. brasiliensis* and *E. melanopterus*. Since the Tobago specimen was identified as *hilarii*, a synonym of *brasiliensis*, and since it seems very probable that *melanopterus* will eventually also be considered a subspecies or synonym of *E. brasiliensis*, the latter name is tentatively used for the Tobago specimen pending a revision of the *E. brasiliensis* group.

16. *Rhogeesa parvula*. Hayman (1938) records this species from Trinidad under the name *R. io*, while Hummelinck (1940) records it from Margarita as *R. minutilla*. According to Hershkovitz (1949), both these forms are only subspecies of *R. tumida*. Hall (1952) considers *tumida* a subspecies of *R. parvula* and hence *io* and *minutilla* are here considered to be additional subspecies of *R. parvula*.

17. *Molossus major*. Hummelinck (1940) has recorded *Molossus* on Curacao, Bonaire, and Margarita as *M. pygmaeus*, while Jones (1951) has recorded *M. obscurus* from Tobago and Grenada. Both of these forms are considered by Hershkovitz (1949) to be subspecies or synonyms of *M. major*. The latter is recorded from Trinidad by Dalquest (1951).

18. *Tadarida brasiliensis*. The United States National Museum has a single specimen (USNM102073) from Tobago. This species is put in brackets at the end of the table because it appears to be the only bat on the islands under consideration which has come from the West Indies rather than from the mainland, the Tobago specimen clearly belonging to the Lesser Antillean *T. b. antillularum* rather than to *T. b. brasiliensis* of South America.

Additional note. As this paper goes to press, an additional paper on Trinidad bats has come to hand (Goodwin, G. G. Three New Bats from Trinidad. Amer. Mus. Novitates 1877, pp. 1–6). In this paper, three additional species are described from Trinidad. Each is clearly quite distinct from any species previously recorded from Trinidad, but appears to be quite close to a related mainland species. Thus *Glossophaga major* appears to represent *G. longirostris* on Trinidad. Regardless of relationships, however, the known bat fauna of Trinidad is certainly increased to 53 species.

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OBSERVATIONS ON THE ECOLOGY OF *PARAMECIUM*, WITH COMMENTS ON THE SPECIES PROBLEM[1]

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INTRODUCTION

It is necessary to make some assumptions in order to make progress in any area of biology, but it would be conceded that the precision of the conclusions is improved with the substitution of certainty for any of the assumptions made. One of the assumptions that is nearly always made in studies on the comparative ecology of different species is that they really represent reproductively isolated populations, or that changes effected by evolutionary forces acting on one cannot be transmitted to the others. The certainty of reproductive isolation has been established in only cases such as *Drosophila, Anopheles,* and a number of vertebrates. One group in which the possibilities remain practically unexplored is the ciliate protozoa, particularly the group of species currently known collectively as *Paramecium aurelia* (Sonneborn, 1938–1957). Although identification of the reproductively isolated groups is somewhat tedious, the act of identification confirms the reproductive isolation, and the results of an ecological study on such a group would thus gain considerable precision. An added advantage of working with *Paramecium* would be that the organisms under investigation are easily grown in the laboratory, and experiments on interspecific relationships could be devised. These experiments could then have more relevance to the field situation than previous experiments on interspecific competition (Gause, Nastukova, and Alpatov, 1934; Park, 1948; Crombie, 1947). Such experiments were planned in conjunction with the present work, which became interrupted before they could be carried out. The original plan of the work was to sample different environments at different seasons in order to discover if obvious ecological differences were present. This information would then be used to plan experiments and more refined sampling. The present paper is a report on the results obtained from the first part of the study.

Sonneborn, who first discovered the existence of the species involved, has continued to use the term "variety" for them rather than to describe them taxonomically, because morphologically distinguishing characters are frequently lacking. In a recent paper (Sonneborn, 1957) he proposes the term "syngen" for these and other such units. Since they are species, I see no point in a new term (see discussion), and throughout the present paper the word variety will be employed because it at least has the status of usage, although Linnaean names would be preferable to the uninitiated.

METHODS AND ERRORS

These preliminary observations were confined to a restricted location which at the same time provided considerable ecological diversity. As the Huron River flows by Ann Arbor, its course is interrupted by three dams. The middle of the three impoundments thus formed lies immediately north of a large wooded tract. A small stream, having its origin in numerous seepage areas in the woods, flows down a rather steep slope into the river. Four river samples were taken within 20

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feet of the mouth of the stream (two upstream and two down), and eight more samples were taken along the course of the stream, including two in separate seepages at or near the stream's origin. The area was sampled on July 1 and October 24, 1952. The October samples were taken from the same spots as the July samples, with the exception that one of the seepages was completely dry and had to be omitted. The temperature of the water was recorded at each site. Each sample consisted of 30 ml. of water and debris from the bottom. As soon as all samples had been collected, they were brought to the laboratory and emptied into finger bowls. They were searched for paramecia immediately, and any that were found were isolated into depression slides. Then all samples were "fed" and allowed to grow. To each sample was added an equal volume of *Aerobacter aerogenes* culture. This culture medium was prepared according to directions given by Sonneborn (1950), with the substitution of Cerophyl (a commercial product consisting of the dried and powdered leaves of cereal grasses) for the baked lettuce.

The samples were searched daily for two weeks, or until paramecia were found. Samples still negative after 14 days were discarded. From each positive sample, three individuals were isolated on the first day of their appearance, three more after the sample was one week old, and three final ones after it was two weeks old. For some samples, circumstances dictated minor deviations from the above pattern. When less than three specimens could be found, another search was made the following day in an attempt to make up to nine the total number of cultures from a sample; in two cases more than three animals were isolated from a sample on a single day; and occasionally specimens were isolated on days other than those indicated above. In a number of cases, less than the desired number could be found, and there was some loss of cultures, as described below.

Following isolation in depression slides, the routine recommended by Sonneborn (1950) was followed. Samples from each culture were stained to confirm identification as *P. aurelia;* individuals were washed to remove foreign bacteria, isolated again in depression slides and eventually transferred to test tubes. Identification was made by mating with known stocks obtained directly or indirectly from Professor T. M. Sonneborn's laboratory. I am indebted to him and to Dr. D. L. Nanney and Dr. N. Melechen for providing me with the stock cultures. Sonneborn's precautions as to controls and adequate amount of mating to establish identification were heeded rigorously.

From the standpoint of sampling error, the method leaves much to be desired, since the practice of subsampling after the wild population had begun to grow would permit slow-growing varieties that were present to be missed. That this may actually have happened is shown by the fact that among the 10 samples where two or more were found, there were only three cases where the less frequent variety was isolated more than once. Hence, the number of discovered cases of common occurrence between the various varieties is very likely an underrepresentation of the actual situation.

Two other possible sources of error have been considered. These are: first, that a significant fraction of paramecia in nature are unable to grow under laboratory conditions, and second, that the period of observation of the sample was insufficient to recover all varieties present. With regard to the first, if it were true there should be more mortality among specimens isolated shortly after collection than among those isolated after a week or more. That this was not true is shown in table 1. The data reflect the experience of the investigator, since losses in

TABLE 1. *Loss of cultures isolated from field samples after various periods in the laboratory*

Date of collection		Number of days after collection								
		0	1	2	3	4	7	8	13	14
July 1, 1952	Number of isolates surviving	2	7	2	8	12	17	21	14	
	Number of isolates dying	1	2	2	4	2	3	4	5	
October 24, 1952	Number of isolates surviving	1	7	5	9		18			12
	Number of isolates dying		2				1			2

October were less than one half as high as in July, when the work started, but there is no reason to conclude that many animals were lost through their own inability to grow in the laboratory.

The possibility of inadequate observation of the samples is apparently disposed of by considering when new information was obtained about them. No sample became positive for paramecia after the seventh day, and no previously undiscovered varieties were obtained after the eighth day. The data for the 13th and 14th days were wasted, except for establishing the adequacy of the period of observation.

RESULTS

The identity of 131 cultures was established by breeding tests. Of these, 79 were obtained from the July samples and 52 from the October ones. Four varieties of *Paramecium aurelia* were obtained, and in addition four cultures were identified cytologically as *P. multimicronucleatum*. This species was reduced to the synonymy of *P. aurelia* in the body of Sonneborn's 1957 paper, but redefined in the appendix. However, in a later part of the appendix he continues to refer it to *P. aurelia*. Although no evidence was obtained about the mating of these four cultures, the information given by Sonneborn indicates a strong probability that what was obtained was his variety 15 of *P. aurelia*. Besides the *aurelia-multimicronucleatum* complex of species, *Paramecium caudatum* was isolated 44 times, appearing only in the river samples, but being present both in July (35 cultures) and October (9 cultures). No attempt was made to identify varieties in *P. caudatum*, although these are well known to exist (Gilman, 1941).

The complete results of the study are given in table 2. The varieties found correspond to expectations based on Sonneborn (1957, Table II and accompanying text) to a degree that is remarkable in view of the limited scope of the present investigation. Ann Arbor is somewhere near the southern part of his "cold" zone, in which he lists varieties 1, 2, 3, 5, 9, 11, and 15 (*P. multimicronucleatum*). Of these, only varieties 9, known only from Europe, and 11, represented in the northern United States by a single sample and typical of the warm zone, are missing from this study. In his "cool" zone immediately to the south, one could reasonably expect variety 4, and it may eventually be found at Ann Arbor, but

TABLE 2. *The number of cultures of each of five varieties of* Paramecium aurelia *obtained at the same locations in July and October*

Sample location		July 1, 1952								October 24, 1952							
		Temp. (°C)	Variety number					Total number of		Temp. (°C)	Variety number					Total number of	
			1	2	3	5	15	Cultures	Varieties		1	2	3	5	15	Cultures	Varieties
River	1	27.0	4	0	3	0	0	7	2	10.5	0	0	1	8	0	9	2
	2	26.5	0	0	1	3	1	5	3	10.0	0	6	0	0	0	6	1
	3	24.5	0	3	0	9	1	13	3	10.5	0	2	3	0	0	5	2
	4	27.0	0	1	1	0	0	2	2	9.5	0	0	0	0	0	0	0
Stream	5	18.0	0	3	0	0	0	3	1	8.5	0	5	0	0	0	5	1
	6	17.0	0	10	0	1	0	11	2	8.5	0	0	0	0	0	0	0
	7	16.5	0	7	0	1	0	8	2	8.0	0	0	0	0	0	0	0
	8	17.0	0	0	0	0	0	0	0	8.0	0	0	0	0	0	0	0
	9	15.0	0	9	0	0	1	10	2	8.5	0	11	0	0	0	11	1
	10*	15.0	0	7	0	0	0	7	1	9.0	0	7	0	0	0	7	1
	11	17.0	0	9	0	1	1	11	3	9.5	0	9	0	0	0	9	1
	12*	16.0	0	6	0	0	0	6	1	Dry							
Total samples per variety			1	9	3	5	4				0	6	2	1	0		
Total cultures per variety			4	55	5	15	4	83			0	40	4	8	0	52	

* Samples from seepa e areas.

it is unlikely that varieties 6 or 8, found once each in the "cool" zone, will appear.

The fauna of the river sites is much richer than that of the side stream, no varieties being found in the stream that were not also present in the river; two (varieties 1 and 3) were found only in the river, in addition to *P. caudatum* with an unknown number of varieties, also confined to the river.

I. POPULATION SIZE

The number of cultures of one variety that are shown from a single sample is not particularly significant, since all could be the progeny of one individual, except in two cases where variety 2 was isolated on the day of collection and also on subsequent days, showing that at least two individuals were present originally. The samples involved were no. 3 in July and no. 9 in October. Aside from these two cases, the meaningful data are in the frequencies of occurrence of the different varieties at different times and places. Had each variety occurred not more than once in samples where it was found, the density of *P. aurelia* would be 1.8 per 30 ml. in July and 0.8 in October. Sonneborn (1957), using the proportion of negative samples in Pringle's (1956) observations and assuming the Poisson distribution, calculated the average density of variety 9 in Scotland as 1 per 40 ml. during the season of maximal abundance. This approach assumes a random distribution, which, as Sonneborn points out, is probably inaccurate, but is more realistic than assuming no cases of more than one occurrence of a variety in a sample. Moreover, since animals generally have a clumped distribution (Hairston and Byers, 1954), the assumption of randomness yields an estimate that still errs towards too low a figure. Assuming the Poisson distribution, the present data give

the estimates shown in table 3. The densities for the different varieties range from a little less than one half of the figure obtained from Pringle's data to a little more than three times as great. They are clearly of the same order of magnitude. It could be argued that because of the few samples involved, these data do not permit a much smaller figure that is still larger than zero, and while this is true of the river samples, the stream samples could yield an estimated mean density as low as 0.15 per 30 ml.—half of the lowest figure actually obtained. While there is some statistical restriction on the low estimates, it does not appear serious, and it seems a valid statement that population densities of single varieties are comparable in Michigan and Scotland. They can surely go higher. In one sample, 27 specimens of *Paramecium caudatum* were isolated on the day of collection—a density of almost 1 per ml., and of course under laboratory conditions populations can become much more dense, although it is doubtful whether such conditions are ever met in nature.

For the whole group, populations were denser in the river than in the side stream both times, but it is interesting to note that this is because of the greater diversity in the river, since on both occasions the greatest density of a single variety occurred in the stream.

TABLE 3. *Estimated mean densities per 30 ml. of five varieties of* Paramecium aurelia *in two situations at two seasons.* Estimates are from the frequencies of negative samples, assuming the Poisson distribution.

Habitat	Variety number	Month	
		July	October
River	1	0.3	0
	2	0.7	0.7
	3	1.4	0.7
	5	0.7	0.3
	15	0.7	0
	Sum	3.8	1.7
Side stream	1	0	0
	2	2.0	0.85
	3	0	0
	5	0.4	0
	15	0.3	0
	Sum	2.7	0.85

II. Temperature Relationships

The data give considerable evidence of the importance of temperature to the different varieties, aside from the general fact that the October samples contained only one half to one third as many paramecia as the July ones. Variety 2 is clearly less sensitive to low temperatures than are the others. In July, its density was three times as great in the cool side stream as it was in the river; it was the only one found in the side stream in October; and its population remained as high in the river in October as it was in July—the only case where the 16° drop in temperature did not result in at least a halving of the population. Variety 1 was most sensitive to low temperatures, never occurring in the side stream and disappearing altogether in October. Varieties 3, 5, and *P. multimicronucleatum* ("variety 15") represent a more complex situation in which temperature is involved, but in which temperature differences appear no more important than other ecological considerations. All are intermediate between varieties 1 and 2 in their response to the temperature differences observed. Variety 5 and *P. multimicronucleatum* are much alike in distribution, and both show a more pronounced seasonal decrease in numbers than variety 3.

III. Other Ecological Differences

From the distribution of the varieties in July, one would expect variety 3 to be more sensitive to cold than any other except variety 1, since they were the only ones confined to the river. These expectations were not realized, as variety 3 maintained its abundance relative to the group as a whole in October, whereas 1

and 5 and *P. multimicronucleatum* decreased more, both on an absolute and a relative scale. Assuming that these differences are not statistical accidents, some factor other than low temperature must prevent variety 3 from invading the side stream. The possible nature of such factors is considered in the discussion.

The histories of the samples after being brought into the laboratory provide some interesting data on relationships, as well as indications for future work. The different varieties tended to appear in sequence (table 4). The average number of days until the first appearance was least in variety 2 and greatest in variety 5 and *P. multimicronucleatum*. Although the early appearance of variety 2 is attributable in part to its greater abundance, it would appear that other factors were also operating. In the seven samples where it was present with other varieties, it was isolated before the others six times and simultaneously once. Combinations of other varieties showed no such regularity. The most obvious reasons for earlier appearance would be greater abundance, noted above, a more rapid rate of multiplication, and an inhibitory effect on other varieties. It appears that the second possibility is likely to be correct only in conjunction with the third, since of five varieties tested at temperatures comparable with those obtaining in this laboratory, variety 2 gave the lowest fission rate (Sonneborn, 1957, p. 176). It must be mentioned that variety 5 and *P. multimicronucleatum* were not included in the experiments, and the possibility of strain differences within the varieties cannot be excluded, as he points out. Some stocks of variety 2, including at least one of the present series, are known to kill other stocks and other varieties, and this could be a factor producing the observed results.

TABLE 4. *Frequency of first appearance of five varieties of* Paramecium aurelia *in 23 samples, after different periods in the laboratory.* Samples were fed after searching on day of collection.

Variety number	Days after collection							Average
	0	1	2	3	4	7	8	
1				1				—
2	3	3	1	3	4	1	0	2.5
3	0	1	2	1	0	1	0	3.4
5	0	1	1	0	0	1	3	5.7
15	0	0	1	0	0	3	0	5.8

DISCUSSION

I. Interspecific Relationships

As meager as the data are, they are sufficient to indicate that the same kind of situation exists among the local varieties of *Paramecium aurelia* and *P. multimicronucleatum* that has frequently been found when investigations were made of closely related species inhabiting the same area. Each one has a characteristic distribution in place and time. The implication is that their requirements are different, and the explanation offered in nearly all such cases is that this is the result of natural selection favoring diversification over competition. In the present case, the requirements are sufficiently alike for all to grow well under identical laboratory conditions, however.

If we regard the seasons and the habitats as separate bases for classification, then there are four season-habitat combinations that could be occupied. Variety 1 is the most restricted, being found only in the river in July. Variety 3 and *P. multimicronucleatum* come next, the former being found in the river both in July and October, and the latter occurring in both river and side stream, but only in July. Variety 5 is missing from only one season—habitat, the side stream in October, and variety 2 occupies all four combinations. It should be admitted that the failure to find a variety in October in a habitat in which it was found in July probably means that the population was at a very low level, rather than that it was really absent. However, our knowledge of the means of spread of *Paramecium* is nil, and until some in-

formation is available on rates of invasion of unoccupied habitats, perhaps we should not assume that winter refuges are necessarily available in all habitats where they are found in summer.

In any case, reduction in numbers through lowered temperatures, which evidently occurred in all varieties, is not a sufficient explanation for all of the data. Variety 2, which suffered a 58% reduction in numbers in the side stream between July and October, showed no detectable difference in the river. It could be maintained that both temperatures were suboptimal for variety 2, whereas July temperatures were nearer the optima of the other four. The difficulty with this explanation lies in the observed earlier appearance of variety 2 in the samples under laboratory conditions, where the temperature approximated that in the river. It would appear therefore that some unidentified factor serves to keep down the population of variety 2 in the river in July.

With variety 3, we have an analogous situation, but with regard to distribution in space rather than in time. This is a cold climate variety according to Sonneborn, and its continued occurrence in the river in October bears this out, especially when it is noted that variety 3 accounts for as large a fraction of all those present in October as it did in July. It thus should occur in the cooler side stream, at least in summer. That it did not when the more cold-sensitive variety 5 and *P. multimicronucleatum* did may be looked upon as evidence that some other factor prevents it from becoming established there.

Two of the five forms, then, are shown to be sensitive to facets of the environment in ways that are peculiar to themselves rather than to *P. aurelia* generally. As to whether these peculiarities relate to the living, rather than the non-living part of the environment, no definite decision can be made as yet, but the former would appear likely, because it is more complex and would provide more opportunities for divergence of closely related but reproductively isolated forms. The physical environment appears to provide the broad categories of habitats and the biotic environment the fine structure of niches. If we grant the likelihood that biotic limiting factors are responsible for the otherwise unexplained information about varieties 2 and 3, it is worth while to consider what their nature might be. Because of the method of feeding and because all varieties grow well on a number of different bacterial species (Sonneborn, 1950), food differences seem to be unlikely. Differential predation would also appear not to operate unless microdistributional differences can be demonstrated —an obvious gap in our information that should be filled by appropriate sampling techniques.

The hypothesis is advanced that the two varieties affect each other unfavorably, and that the influence of variety 3 is greater under conditions obtaining in the river in July, but that variety 2 is favored by conditions in the side stream at all times and that these conditions are approached in the river during autumn. It is possible to envision a situation in which a net balance could be maintained, as for example by the annual temperature changes, a higher temperature favoring variety 3, a lower one favoring variety 2 (cf. Hutchinson, 1944). Actually, the situation is probably more complex, but experiments could be devised to test the hypothesis as far as temperature, rate of feeding, and kind of food are concerned. Although many similar competition experiments have been performed, those proposed here would have the merit of a more realistic relationship to an actual field situation.

II. What is a Syngen?

In his long and stimulating treatise on "Breeding Systems, Reproductive Methods, and Species Problems in Protozoa," Sonneborn (1957) devotes part of the

paper to the question of whether the subunits of various ciliate species, known for nearly 20 years as "varieties," should be considered species and given names under the system of binomial nomenclature. He points out, as he has consistently done since his first discovery of their existence (Sonneborn, 1938–1957), that the varieties in fact correspond closely to the concept of species as envisioned by most present-day biologists. After considering the problem at length, he concludes that the varieties should not be given species names, and moreover that our whole way of looking at the problem should be revised. He proposes that we abandon the current general attempt to equate taxonomic entities with reproductively isolated populations, and that we freely recognize a fundamental distinction between the biological species and the species of taxonomists. He then points out that this position requires either that we have two definitions for the word species or that a new word be coined for one of the two entities. Conceding the word species to the taxonomists on the grounds of priority and generality, he proposes the term *syngen* (generating together) for the reproductively isolated population. Sonneborn gives several reasons for taking this position, and since I do not agree that they are convincing, I shall discuss each one.

His first point is that the widespread and frequent occurrence of asexual and obligate inbreeding forms restricts the applicability of the biological species concept to perhaps a "minority of all organisms." Now, while such forms may not be rare, the fraction of organisms thus excluded in principle from the biological species concept is open to question. The relatively recent discoveries of sexual phenomena in bacteria, viruses, trypanosomes, and fungi imperfecti would seem to place the burden of proof upon anyone who would claim the absence of sex in any given form. Sonneborn's own work has shown the necessity of providing the proper conditions for mating to take place, and the fact that sexual behavior has not been observed may be a reflection of the failure to provide these conditions or to recognize sexual phenomena when they occur. How many protozoans have been tested at temperatures lower than 19° C in the dark? These are two of the necessary conditions for mating in variety 2 of *Paramecium aurelia*. Would we recognize mating in *Amoeba* if it took place? The success with bacteria and viruses is due to their amenability to mass culture and plating techniques, and even with these the demonstration of recombination was long delayed. In view of the recent successes, I would argue that completely asexual or obligate inbreeding forms are not sufficiently common to reduce seriously the applicability of the biological species concept.

The next point raised is that some currently recognized taxonomic species would have to be subdivided into "fantastically large numbers of 'biological' species" which would be "unidentifiable by routine taxonomic procedures or by any other procedures that could reasonably be expected of working biologists." The first part of this argument seems merely a complaint about the complexity of nature. The second part is more worthy of debate. Having done the research reported above, I am thoroughly aware of the difficulty of properly identifying a wild specimen of *Paramecium aurelia*. I do believe that I qualify as a working biologist, and I found it possible to make the identifications by following Sonneborn's (1950) instructions. The work required about nine months, but was proceeding much more rapidly when interrupted. Having spent at least a comparable amount of time learning the taxonomy of about 20 different Southern Appalachian salamanders (Hairston, 1949–1951; Pope and Hairston, 1947, 1948; Hairston and Pope, 1948), I am not prepared to concede that the two tasks

are orders of magnitude apart in effort required. Sonneborn emphasizes the fact that he has spent 20 years working out the currently recognized varieties. His other accomplishments during those 20 years indicate that considerably less than that time was actually spent working out the system of varieties. Moreover, it was pioneering work—always time-consuming. We must also consider the rapidity with which it resulted in the understanding of varieties in other ciliates.

But to return to the main argument, Sonneborn seems to assume that the existing fauna consists of either "readily recognizable" taxonomic species or of forms too difficult for the working biologist to identify. As a matter of fact, there is a complete gradation in ease of identification from male warblers in spring to the varieties of the ciliate *Tetrahymena pyriformis,* in which the mating reaction is the only discovered criterion that separates them. *Paramecium aurelia* admittedly stands near the difficult end of the scale, but nevertheless possesses taxonomic characters. According to Sonneborn, size and micronuclear form alone will subdivide the 16 varieties into five known categories. To select a group somewhat more nearly intermediate, the European mosquitoes of the *Anopheles maculipennis* complex are not separable on the basis of adult characters except for an average difference in one case and a hardly discernable difference apparent only on newly emerged specimens in another, but can be distinguished readily on the basis of their eggs (Hackett, 1937). Reproductively, they are remarkably like the varieties of *P. aurelia,* hybrids being obtainable in some cases, but effective gene flow being impossible between them. There is thus no criterion by which a decision can be made as to whether a group of species or a group of syngens is being dealt with. Sonneborn would restrict the term species to "Groups of organisms that are judged to show minimal, irreversible, visible divergence . . ." He is required by his own definition to recognize at least three undescribed species in the *aurelia-multimicronucleatum* complex, since five such entities exist and only the two names appear to be applicable. The immediate difficulty with this approach is that it cuts across more profound biological differences. Thus, varieties 2 and 6 would be placed taxonomically with varieties 1, 3, 5, 7, 9, and 11, although the weight of biological evidence places them with varieties 4, 8, 10, and 14. He would thus deny that evolutionary affinities however ascertained should always be considered in reaching decisions about the catalog of nature, and this I consider to be the heart of the whole argument. To deny the goal of understanding, however remote or seemingly unattainable, is to deny the existence of a science. This denial is apparently based either upon a freely confessed ignorance of the field or upon a mistrust of methods in which inferences are drawn from a consideration of the phenotypic characters possessed by individuals. It is conceded that this method has a higher probability of error than the technique of experimental mating, but it must be recognized that the latter is also subject to error. *Peromyscus leucopus* and *P. gossypinus* cross in the laboratory and produce fertile offspring (Dice, 1937), although in at least one area of natural overlap of their ranges no intermediates are found (Dice, 1940). Thus, whatever they could do, they actually fail to exchange genes. For a considerable period, the attempt has been made in taxonomy to approximate the reproductively isolated population by inference from phenotypic characters. Regardless of the success achieved, it has been a stimulating influence and has been the interpretive basis for work in all areas of taxonomy. In place of this, Sonneborn proposes to reduce the term to something "primarily designed for the convenience of biologists and . . . not intended to represent a biological reality." I am at a loss to know

what kind of biologist would find such a term convenient. Not the taxonomist, who is trying to represent the animal kingdom in as logical a manner as possible and who needs evolution as a framework and the reproductively isolated population as an objective base; not the physiologist, the ecologist, or the embryologist, who deal with the multiple results of natural selection and who should know or make assumptions about the possibilities for recombination among the units with which they work; and certainly not the geneticist, whose field has contributed so much to understanding the processes by which species become distinct.

The current anomalous situation in which a species of protozoans is the equivalent of a genus or subgenus of most other well-studied animals clearly needs correcting. Sonneborn is certainly the person to correct it, but accepting his present proposals would only add confusion to an already jargon-ridden branch of science.

Summary

Studies were conducted on the comparative ecology of the "varieties" of *Paramecium aurelia* by sampling an impounded stretch of a river and a small seepage-fed tributary stream. Samples were taken July 1 and October 24, 1952. The act of identification of the varieties confirms their reproductive isolation from one another. This point is assumed but not tested in most ecological studies.

Five varieties (1, 2, 3, 5, and 15) were identified. All occurred in a 40-foot stretch of the river, and varieties 2, 5, and 15 were also isolated from the small stream. Variety 2 occurred in both locations both times; variety 5 was present in both river and stream in July, but was only present in the river in October. Variety 3 was confined to the river, where it was the commonest form in July, and equal to any other in October. Variety 15 was only collected in July, but was present in both locations. Variety 1 was found in a single river sample in July. Each variety has a characteristic distribution in time and space. Many, but not all of these distributions can be explained on the basis of different sensitivities to temperature differences, but this explanation is not sufficient in the cases of varieties 2 and 3. The hypothesis is advanced that they are exercising an inhibitory effect on each other, conditions in the side stream favoring variety 2 and those in the river, particularly in July, favoring variety 3.

Sonneborn's suggestion that reproductively isolated populations (the species of most biologists) be distinguished from taxonomic species by the separate name of "syngen" is examined in detail. It is concluded that the suggestion is not justified, and that biology would be served best if all such units were recognized as species and given Linnaean names.

Addendum

The appearance of the description by Diller and Earl of *Paramecium jenningsi* (*J. Protozool.*, **5** (2): 155–158.) after the foregoing remarks were in press provides an example of the unfortunate consequences of not having an orderly system of naming the varieties in a taxonomically acceptable manner. Incredible as it seems, they were apparently unaware of the range of variation in *P. aurelia* as set forth by Sonneborn. It is likely from their data that one of the smallest varieties of *P. aurelia* was used for size comparisons, although the nutritional state is not given, which prevents a good comparison with Sonneborn's figures. They fail to distinguish their new species from variety 12, especially in the size and structure of the micronucleus, and although the mean length of *P. jenningsi* is less than that of variety 12, there is overlap in the values. They give no data on mating reaction with any other stocks, and therefore variety 12 must be assigned tentatively to *P. jenningsi*,

thereby extending the range of the latter to Madagascar. Had a logical, taxonomically acceptable system been established prior to the publication of this new name, the break in continuity beween variety numbers and names could have been avoided easily.

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EVOLUTION AND BIOGEOGRAPHY OF THE APLODONTID AND MYLAGAULID RODENTS

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Introduction

Mylagaulid and aplodontid rodents are common members of late Tertiary faunas in the Great Basin of Western North America. The morphologic and distributional changes of these two closely related groups have been of interest to many workers. The discovery of new forms and the opportunity to study all the material from the Great Basin has resulted in the solution of some of the problems concerning these rodents. The fact that the geographic area of this study is the apparent center of origin of both families as they are known in their latter history makes the results even more interesting.

This study is limited largely to the Great Basin for several reasons. The basin remains a large single biological province during the period of time of interest in this study even though it experiences profound climatic change. It is near if not the center of origin of these families. It is the area of investigation of a much broader problem of which the present study is but a small part. Fossil evidence of the aplodontids is almost entirely from this area. It is hoped that although mylagaulids are of a much more extensive distribution a study of their succession in this particular area will result in a picture of their developmental trends. Understanding these developmental trends may allow the use of these rodents as stratigraphic indicators.

The map (fig. 22) shows the location of the various faunas which contain aplodontid or mylagaulid rodents in Western North America. These faunas range in age from Arikareean (early Miocene) to Hemphillian (middle Pliocene). They lack only Hemingfordian (middle Miocene) examples to present a complete sequence. This study is not a taxonomic review but an attempt to discover developmental trends among the variations present in mylagaulids and aplodontids and incorporate this with their distribution changes into an historical biogeographic picture of these rodents.

Aplodontidae

The family aplodontidae which includes the living mountain beaver of the Pacific Northwest has received attention from a number of workers. Cope (1878) and Marsh (1877) described some of the first known fossil forms from the John Day beds of Oregon. Later Furlong (1910), Schlosser (1924), Gazin (1932), Stock (1935), and Macdonald (1956) described new forms from Oregon, Nevada, California, and Asia. The significance of these finds and the relationships of the known forms have been discussed by Gazin (1932), Stock (1935), Wilson (1937) and McGrew (1941).

Although the present study is more concerned with distributional characteristics of the family than taxonomic problems, some systematic relationships must be discussed in order to fit new material into a developmental sequence. This concerns the middle and later Cenozoic aplodontids in particular.

The family mylagaulidae arises out of the aplodontidae in the early Miocene or late Oligocene from *Meniscomys* or something very much like it. *Meniscomys* is usually classified as an aplodontid but might just as well be included in the mylagaulidae since it presents all the basic characteristics expected of an early my-

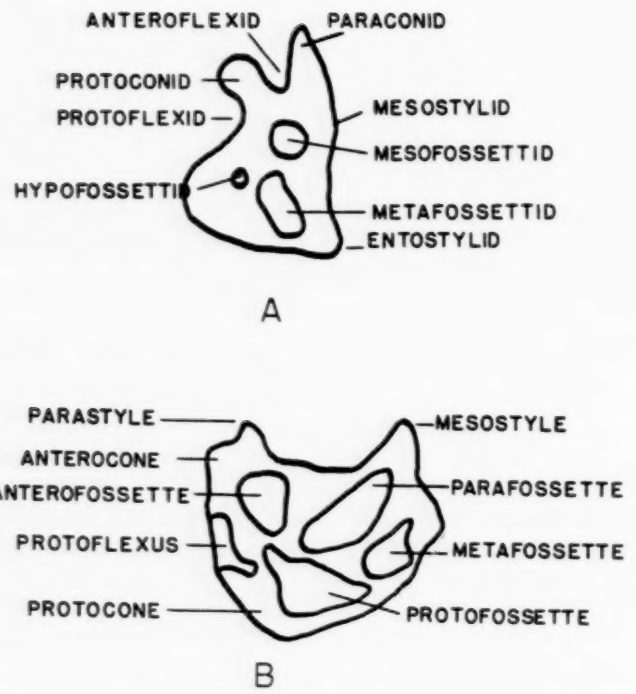


FIG. 1. Nomenclature of aplodontid teeth. A, lower left P4, B, upper left P4.

lagualid. For this reason *Meniscomys* will be discussed under that family. The Arikareean (earliest Miocene) is an important time in aplodontid and mylagaulid development for the purposes of the present study. It is at this time that both families first display the basic characteristics of their later Cenozoic representatives. For the expressed purposes of this study this is essentially the beginning although the earlier history is referred to when it is significant to the present problem.

The nomenclature used in the discussion of the aplodontids is shown in figure 1.

Sewelleladon predontia N.g., N. sp.

Holotype: Left lower jaw with P4-M3, UOMNH F-4734, fig. 2.

Type Locality UO 2275, in lower upper John Day Formation along Haystack Creek, in Wheeler Co., Oregon, from a small slump block in the valley of a small north branch of Haystack Creek in section 21, T8S, R25E, three miles Northeast of Spray, Oregon.

Diagnosis: A rooted aplodontid with an anteroflexid bifurcating the face of the lower fourth premolar, the largest tooth of the cheek tooth series. Moderately high crowned teeth and a well developed masseteric ridge.

Lower dentition: The fourth premolar is the largest tooth of the series. Sharp styles extend the full length of the anterior faces of the protoconid and paraconid, much like later aplodontids. Short metastylid also present. A

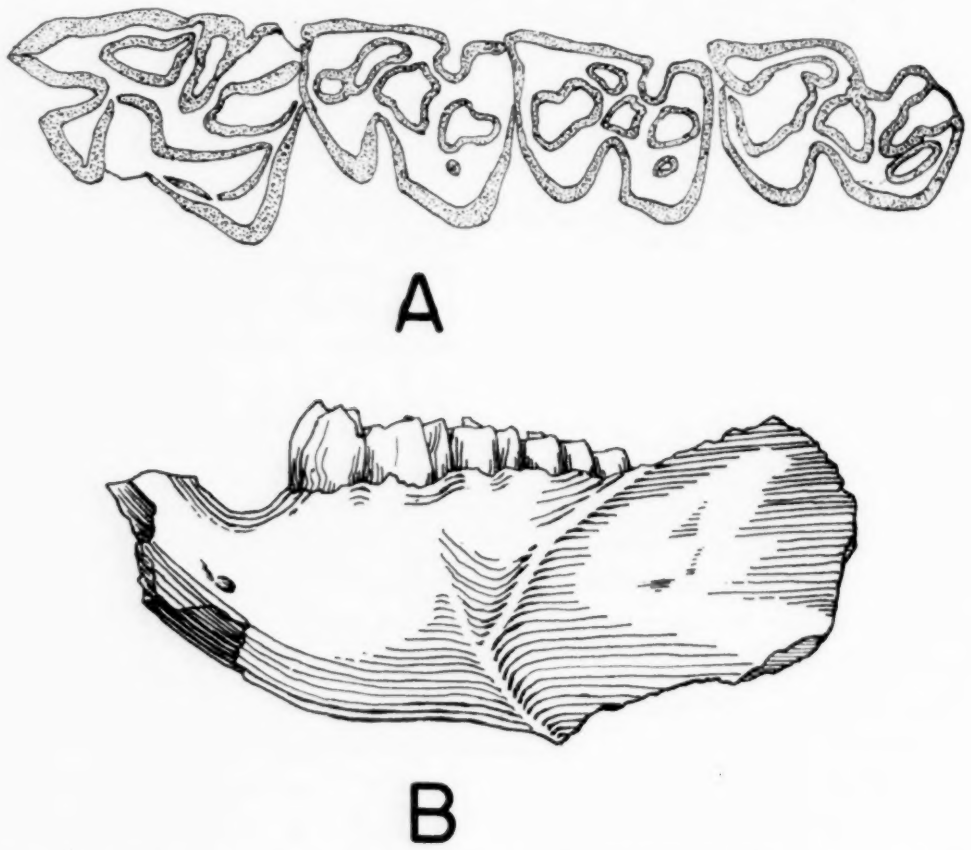


FIG. 2. Type of *Sewelleladon predontia*, UOMNH F-4734. A. Occlusal view of dentition, × 8. B. Labial view of left jaw, × 3.

lake in the position of the parafossettid is apparently a pinched off part of the anteroflexid as seen in the molars. The anteroflexid does not close to form a fossettid. The mesoflexid is directed almost transversely across the tooth tending slightly anteriorly. It appears to be bifurcated below the present occlusal surface which, on wear, would result in two small lakes one median to the other. The more central one probably is short lived. The metaflexid is directed postero-anteriorly and probably would result upon wear in a persistent metafossettid. The hypo and protoflexids have a common opening to the labial side of the tooth. With a little wear they would soon be separate lakes. The protofossettid may be divided on wear as is the mesofossettid into two small lakes. The premolar is rooted and not much more high crowned for its relative size than is the premolar of *Meniscomys*.

The molars differ from each other only in their stage of wear. The last molar is least worn. There apparently is no mesoconid. The hypoconid and protoconid are very well developed. The entoconid is a distinct almost bulbous cusp isolated in early wear from the hypoconid and connected with the metaconid only in late wear. The typical molar in moderate wear exhibits a protoflexid and mesoflexid. The lake pattern in worn teeth consists of a long bifurcated lake in the trigonid, a single lake between the protoflexid and mesoflexid, probably derived from the mesoflexid, and two lakes in the talonid, one rather persistent and one less persistent both derived from the metaflexid. Considerable wear would likely result in a pattern of three lakes in an antero-posterior line as in *Meniscomys* and *Liodontia*. Internal styles on the P4-M3 are present but poorly developed.

Lower jaw: The jaw is about the size of that of *Liodontia*. All the teeth are rooted. The masseteric ridge is about as well developed as in *Liodontia* and *Aplodontia* and much more so than in *Allomys* or *Meniscomys*. The dental foramen is in the same position as in *Aplodontia*. The incisor ends directly below the third molar and has a slightly curved face. The angle of the jaw is missing, the coronoid process leaves the alveolar region between the second and third molars.

Measurements

	AP	T
P4	3.4	2.6
M1	2.3	2.2
M2	2.4	2.1
M3	2.8	2.1
P4–M3	11.7	
Incisor		1.8

Comparisons: The new genus differs from *Meniscomys* in the development of a full length anteroflexid bifurcating the anterior face of the premolar. The lake in the position of a parafossettid is not seen in *Meniscomys*. The new genus is larger and the teeth more hypsodont. *Sewelleladon* is not a mylagaulid. This is most evident in the development of a completely open anteroflexid and the appearance of prominent styles bordering the anteroflexid, characters distinctly aplodontid. The new genus is larger and higher crowned than *Allomys* and does not have the complicated fossettid borders of that genus. It is most like *Liodontia* among post *Meniscomys* aplodontids and is a good intermediate between *Meniscomys* and *Liodontia* possessing characters of both. It differs from *Liodontia* in its rooted lower crowned teeth.

Sciuridon

This rodent from Europe has been classified with the aplodontids (Stehlin and Schuab, 1951; Dehm, 1950). Piveteau (1934) went so far as to consider *Sciuridon* and *Allomys* synonymous. Both forms display highly complex dental patterns. They differ significantly however in the relative size of the teeth. In *Sciuridon* the lower fourth premolar is much smaller than the other cheek teeth and the upper fourth premolar about the same size as the other upper cheek teeth. This is characteristic of many sciurids. The lower fourth premolar of *Allomys* is as large or larger than the other cheek teeth while the upper fourth premolar is larger than the other upper cheek teeth. This is typical of aplodontids and castoroids. It seems likely then, that *Sciuridon* may be a parallel development of high complexity rather than a related form as suggested earlier by Taylor (1918).

Ameniscomys selenoides Dehm

Another possible European occurrence of an aplodontid is that of *Ameniscomys selenoides* reported by Dehm (1950). This species which is described as close to *Meniscomys* of North America is much more aplodontoid than *Sciuridon*. It possesses the open anteroflexid in the lower premolar and little worn molars so characteristic of aplodontids. The upper premolar has a much more squared off lingual border than does *Meniscomys*. It does not appear from the illustrations that *Ameniscomys* has the well developed L-shaped hypo-parafossette of *Meniscomys*. The available evidence does not allow a clear decision on the affinities of this form.

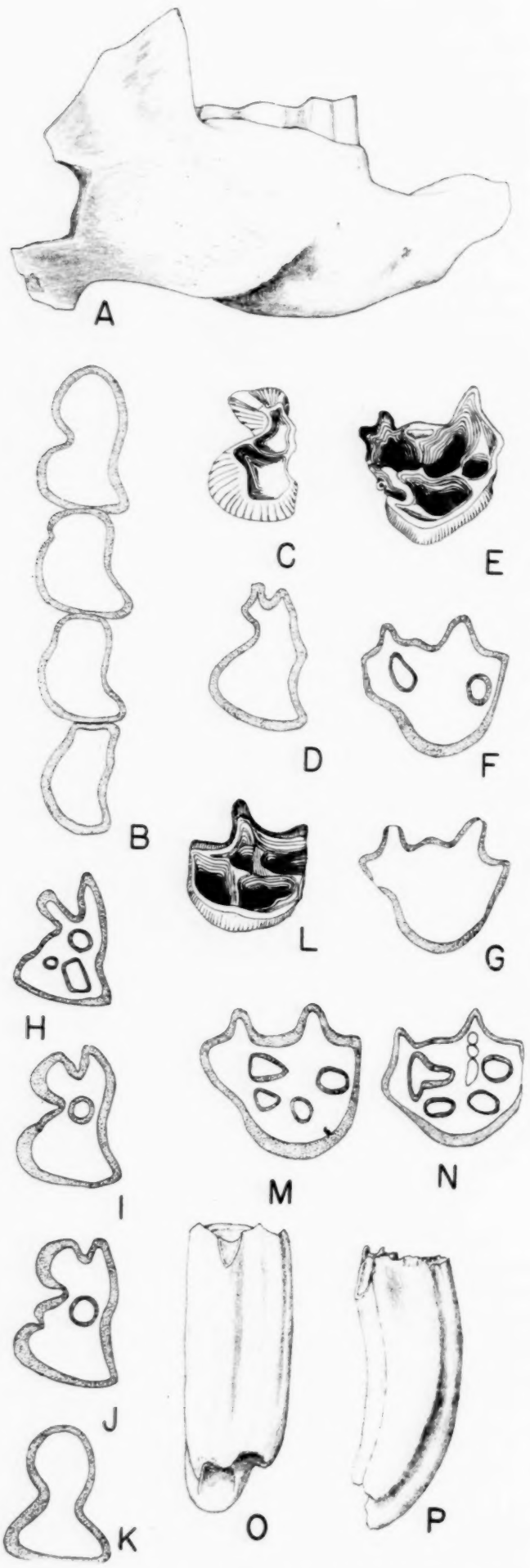


FIG. 3. A. Right lower jaw of *Liodontia furlongi*, UC, × 2. B. Well worn lower left P4-M3 of *Liodontia furlongi*, UC11807, × 5. C. Unworn lower left P4 of *Liodontia furlongi*, UC11909, × 5 (from paratype). D. Moderately worn lower left P4 of *Liodontia furlongi*, UC31065, × 5. E. Unworn upper left P4 of *Liodontia furlongi*, UC11899, × 5. F. Moderately worn upper left P4 of *Liodontia furlongi*, UC35623, × 5. G. Well worn upper left P4 of *Liodontia furlongi*, UC Loc. 1103, × 5. A–G. From Thousand Creek, Nevada. H. Little worn lower left P4 of *Liodontia alexandrae*, Skull Springs, Oregon, CIT 331, × 5. I. Moderately worn lower left P4 of *Liodontia alexandrae*, Skull Springs, Oregon, CIT 327, × 5. J. Moderately worn lower left P4 of *Liodontia alexandrae*, Skull Springs, Oregon, CIT 328, × 5. K. Well worn lower left P4 of *Liodontia alexandrae*, Skull Springs, Oregon, CIT, 330, × 5. L. Unworn upper molar of *Liodontia alexandrae*, Skull Springs, Oregon, CIT, × 5. M. Moderately worn upper left P4 of *Liodontia alexandrae*, Skull Springs, Oregon, CIT 323, × 5. N. Little worn upper left P4, *Liodontia alexandrae*, Paulina, Oregon, YPM, × 5. O–P. Labial and anterior views of N demonstrating partially closed pulp cavity.

Liodontia alexandrae (Furlong)

Aplodontia alexandrae Furlong, 1910, Univ. Calif. Pub. Geol., Vol. 5, No. 26, p. 398.

Liodontia alexandrae Miller, G. S. & J. W. Gidley, 1918, Jour. Wash. Acad. Sci., Vol. VIII, No. 13, p. 440.

Liodontia alexandrae Gazin, C. Lewis, 1932, Carn. Inst. Wash. Pub. 418, p. 63.

Liodontia alexandrae was originally described from the Virgin Valley fauna of Northern Nevada. It is a common member of the Skull Springs fauna of southeast Oregon and the Beatty Butte fauna of south central Oregon. A single specimen is known from the Paulina Creek locality of east central Oregon. All of these faunas are of Barstovian Age (later Miocene) (fig. 3H–3P).

The lower fourth premolar of this species has a broad entostylid and a slight mesostylid. The lower molars have prominent entostylids and small parastylids. The upper fourth premolar has both meso and parastyles while the molars have only a single enlarged mesostyle. Figures 3H–3P illustrate other characteristics of this species and variations in pattern accompanying wear.

In all material seen the pulp cavity is partially closed by the time the tooth is erupted. Although *Liodontia alexandrae* has hypsodont, high crowned teeth, they have not reached the stage of the ever-growing tooth.

Liodontia furlongi Gazin

Aplodontia alexandrae Furlong, 1910, Univ. Calif. Pub. Geol., Vol. 5, No. 26, p. 398.

Liodontia furlongi Gazin, C. Lewis, 1932, Carn. Inst. Wash. Pub. 418, p. 64.

Liodontia furlongi was described from the Thousand Creek fauna of Northern Nevada. It is best known from this locality. It is also known from two localities in the Juntura basin of southeast Oregon. These are all Hemphillian faunas (fig. 3A–3G).

The lower fourth premolar is similar to *L. alexandrae* but with a more prominent and sharper entostylid. The anteroflexid is never as deep in the occlusal outline as in *L. alexandrae*. The lower molars generally are similar to those of *L. alexandrae;* however, they differ in several respects. There is never a parastylid developed to the extent of that in *L. alexandrae*. The entostylid is more prominent than in *L. alexandrae*.

The upper third premolar is a peg-like tooth. The fourth premolar exhibits antero, para, meta and protofossettes. There is an open portion of the protoflexus in the unworn tooth. The anterostyle and parastyle are well developed, the parastyle the more prominent. There is also a prominent mesostyle. There is a low style between the para and mesostyles which persists through all stages of wear. This style is not present in *L. alexandrae*. The upper fourth premolar of *L. furlongi* differs further from *L. alexandrae* in that it is narrowed lingually so that the occlusal outline is somewhat heart-shaped. In *L. alexandrae* the lingual border of the tooth is broadly rounded in occlusal outline. (See fig. 3E–3G.)

Of the large number of loose *L. furlongi* teeth examined in no instance was there any evidence of partial or incipient closure of the pulp cavity, an apparent universal characteristic of *L. alexandrae*. The Hemphillian *L. furlongi* had then developed an ever growing tooth as is seen in the living *Aplodontia*.

Aplodontia rufa (Rafinesque)

The living mountain beaver exhibits strong mesostylids and entostylids on both permanent and deciduous lower fourth premolars. The deciduous teeth are rooted. The lower molars have well developed metastylids and somewhat lesser developed entostylids. The metastyle of the upper fourth premolar is very prominent whereas the anterostyle is less prominent. An entostylid is present. On the upper molars a strong mesostyle is present accompanied by a very small entostylid. Changes in pattern in the course of wear are illustrated in figures 4C–4H.

Tardontia occidentale (Macdonald) n.g.

Pseudaplodon occidentale Macdonald, 1956, Jour. Paleo., Vol. 30, No. 1, pp. 186–202.

Macdonald (1956) described a rooted aplodontid from the Brady Pocket locality of Western Nevada (UC Locality V4845) of Clarendonian age. This species is designated by the present writer as the genotypic species of *Tardontia*. This species is from older beds than *Pseudaplodon asiatica* yet has high crowned teeth whereas those of the asiatic genus are low crowned. It is not likely then, that the asiatic species could be a descendant of the Nevada species. An earlier species of *Tardontia,* described below, is found in southwestern Nevada. It is a lower crowned form than *T. occidentale,* but still is higher crowned than *P. asiatica.* In both the Nevadan species the lower third molar is longer than the other molars, the first and second molars are about equal in size. In *P. asiatica* the first molar is the largest molar, the second and third are much smaller, the third is the smallest. *Pseudaplodon* and *Tardontia* both have open metaflexids apparently the full length of the tooth in the third molar. Both have rooted teeth and a more or less prominent protoflexid on all the cheek teeth. These later remarks suggest that the two genera discussed are distantly related, the earlier remarks indicate they are, however, probably not in an ancestral relationship one to the other (fig. 5A–5C).

Only elements of the lower dentition are known. In the little worn fourth premolar there is an open anteroflexid which extends to the bottom of the anterior face of the tooth. A small mesofossettid is present as well as a large hypofossettid and a small metafossettid. The tooth is rooted. Meso and entostylids are present. The para and entostylid are prominent in the molars giving a curved lingual border. This is interrupted by a lesser developed mesostylid.

The third lower molar is similar to the others except in the open metaflexid. It is open to the base of the tooth. All the teeth are well rooted apparently as soon as they erupt.

T. occidentale differs from the Stewart Springs species in the much higher crowned teeth and the reduction of the protoflexid in the molars.

?Tardontia cf. *occidentale*

Konizeski (1958) has listed a single tooth of *Pseudaplodon* in a Clarendonian fauna from the Bitterroot Valley of Ravalli County, Montana. Since the specimen is compared to *P. occidentale* I assume that it belongs to the new genus. The specimen was not illustrated and the author has not seen the specimen.

?Tardontia cf. *occidentale*

A rooted upper fourth premolar of an aplodontid was collected from Clarendonian (lower

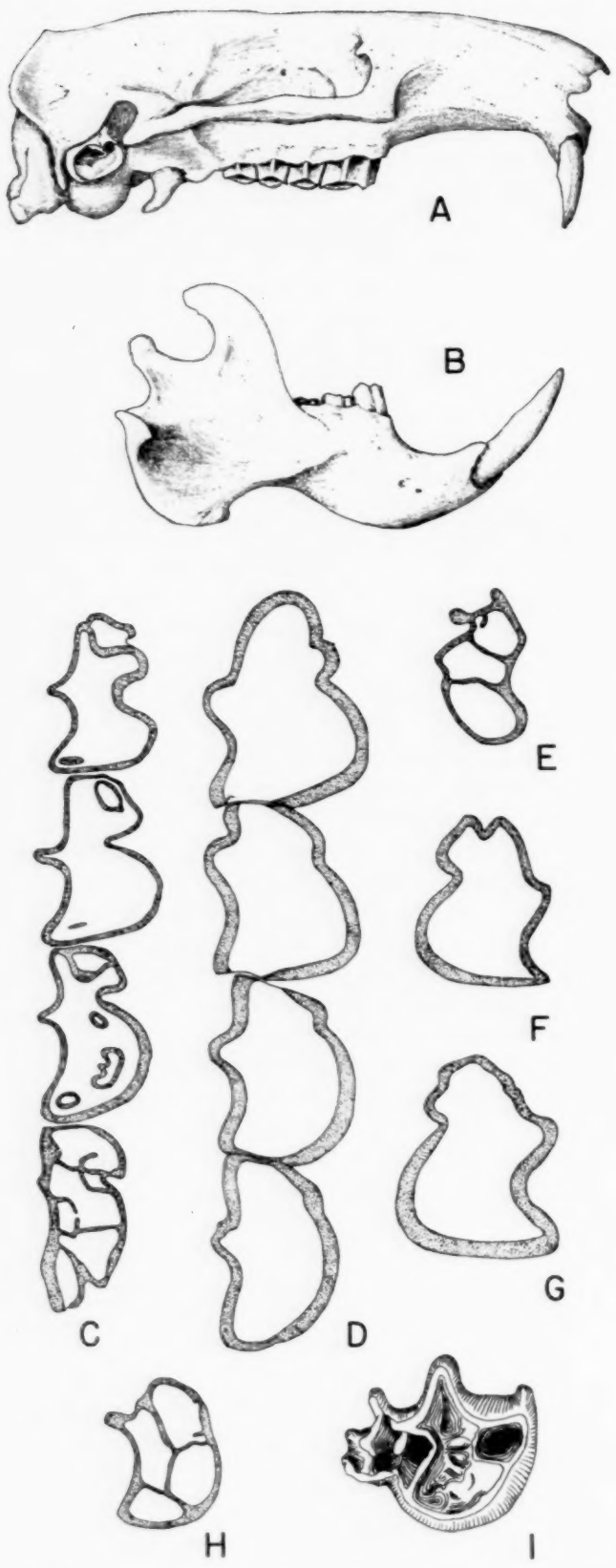


FIG. 4. *Aplodontia rufa.* A. Skull *Aplodontia rufa,* UOMNH 1180, × 1. B. Right lower jaw of *Aplodontia rufa,* UOMNH 1180, × 1. C. Little worn right lower cheek teeth of *Aplodontia rufa,* DP4-M3, UOMNH 724, × 5. D. Well worn right lower dentition *Aplodontia rufa,* P4-M3, UOMNH 1271, × 5. E. Unworn left lower P4 *Aplodontia rufa* UOMNH 724, × 5. F. Moderately worn left lower P4 *Aplodontia rufa,* UOMNH 1429, × 5. G. Well worn left lower P4 *Aplodontia rufa,* UOMNH 941, ×5. H. Unworn right upper M3 of *Aplodontia rufa,* UOMNH 724, × 5. I. Unworn upper left P4 *Aplodontia rufa,* UOMNH 724, × 5.

Pliocene) beds near Juntura, Oregon. It probably represents *T. occidentale.* Unfortunately the specimen was lost. The Juntura fauna is similar to the Brady Pocket fauna in many other ways.

Tardontia nevadans n. sp.

Aplodontia? n. sp. Merriam, J. C., 1916, Univ. Calif. Pub. Geol., Vol. 9, No. 13, p. 177.
Meniscomys Stirton, R. A., 1932, Science, Vol. 76, No. 1959, p. 61.
Liodontia alexandrae? Gazin, C. L., 1932, Carn. Inst. Wash. Pub. 418, p. 67.
Liodontia cf. *alexandrae* Wilson, R. W., 1937, Carn. Inst. Wash. Pub. 487, p. 42.
Holotype: Left lower jaw with M1–M3, UC 31454, fig. 5D–5E.
Paratype: Upper left fourth premolar, UC 19798, fig. 5G–5H.
Type locality: UC loc. 2027, Stewart Springs, Nevada.
Diagnosis: A rooted aplodontid with lower crowned teeth than *T. occidentale.*
Age: Barstovian (later Miocene).

All other published references to the material described here have been based on a single upper fourth premolar. In the collections at UC there is also a lower jaw fragment containing M1–M3. The later material was apparently not seen by earlier workers. The first and second lower molars are rooted and the third which is unerupted is without roots but probably developed them at about the time it was erupted. On the basis of study of the upper fourth premolar (UC 19798) Merriam (1916) concluded that it represented a permanent tooth, not a milk tooth, of an unknown genus somewhere in its relationships between *Meniscomys* and *Aplodontia* in development. Stirton (1932) in a brief summary of the fauna of Stewart Springs (Cedar Mountain) refers to the specimen as representing *Meniscomys.* Gazin (1932) and Wilson (1937) both refer to the specimen as a milk tooth of *Liodontia alexandrae.* Merriam indicated as does the present author that the roots are not comparable to those of the milk teeth of known aplodontids because they are vertically directed. Stirton apparently agreed with this in his reference of the material to *Meniscomys.* The discovery of a lower dentition with rooted molars apparently of the same species and from the same locality further indicates that the rooted upper premolar is a permanent tooth. This tooth then is the only upper dental element known of the new genus.

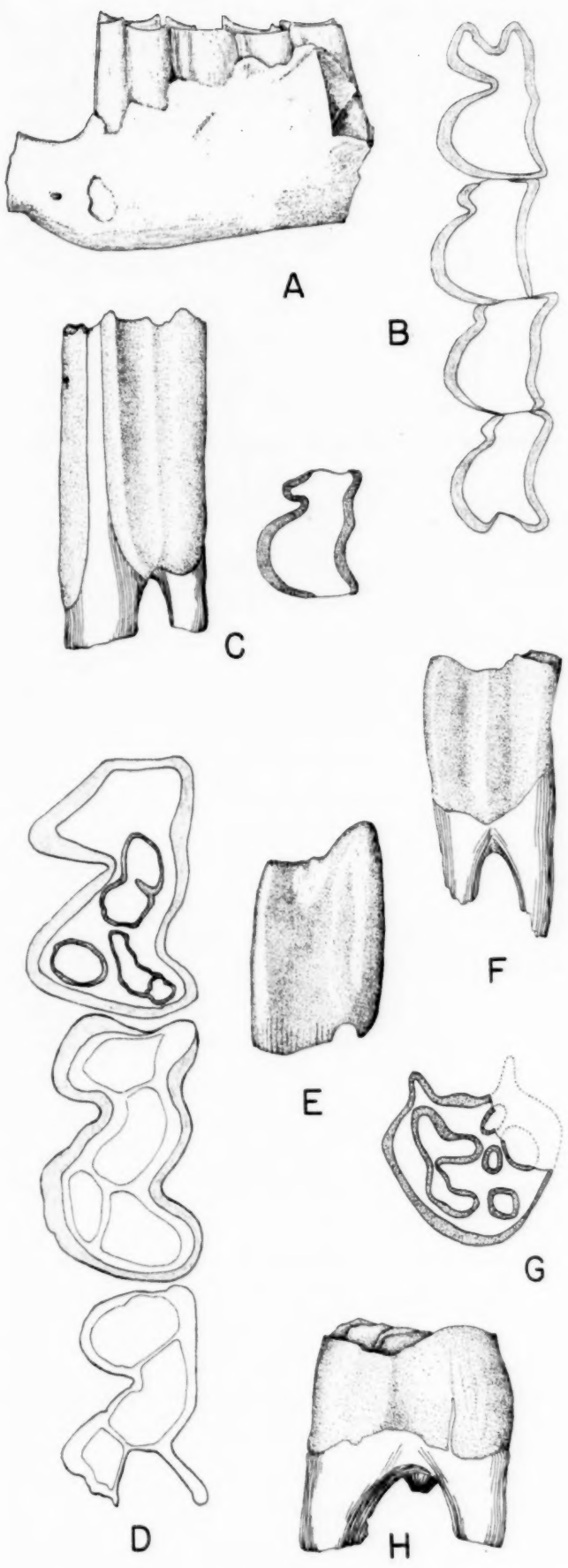


FIG. 5. A. Left lower jaw (type) *Tardontia occidentale,* Brady Pocket, Nevada, UC 38662, × 2.5. B. Occlusal view of A, × 5. C. Lower left M1 or M2 antero-lingual and occlusal views, *Tardontia occidentale,* Brady Pocket, Nevada, UC44738, × 5, illustrating root development and enamel failure. D. Occlusal view M1–M3 type of *Tardontia nevadans,* Stewart Springs, Nevada, UC 31454, × 10. E. Lingual view of unerupted M3 of D illustrating lack of roots at this ontogenetic stage, × 5. F. Lingual view of M1 of D illustrating development of roots in erupted teeth, × 5. G. Occlusal view upper left P4 of *Tardontia nevadans,* Stewart Springs, Nevada, UC19798, × 5. H. Antero-lingual view of G illustrating root development, × 5.

The first and second lower molars have, in little worn teeth, antero, meso, meta and hypofossettids. The anterofossettid is soon lost with wear. The metafossettid breaks down into two small lakes as does the mesofossettid. The protoflexid is deep and extends the full length of the tooth. The labial edge of the protoflexid is angular. The lingual border of the anterior moeity is sharply angular in little worn specimens but becomes somewhat rounder with wear. The posterior moeity has a rounded lingual border. Reduced para, meso and entostylids are present in little worn teeth and are lesser in worn teeth. The first and second molars are well rooted in early wear. (See fig. 5D–5F.) The third lower molar differs from the other primarily in the failure of the metaflexid to close. It is open the entire length of the tooth. The third molar figured (fig. 5D–5E) is apparently unerupted and has not yet developed roots.

The upper premolar is quite similar to that of *Meniscomys* in that it shows connected antero and protofossettes, remains of a hypofossette (2 small lakes in tack) and a metafossette. The parafossette probably was contiguous or nearly so with the hypofossette in earlier wear. The hypofossette is apparently part of the protofossette of later aplodontids or lost completely (fig. 5G–5H).

UC 31454	AP	T (measurements at occlusal surface)
M1	2.7 mm	1.9 mm
M2	2.7 mm	1.7 mm
M3	2.7 mm	1.5 mm

Pseudaplodon asiatica (Schlosser)

Aplodontia asiatica Schlosser, 1924, Paleo. Sinica, S. C., Vol. 1, f. 1, p. 30.
Pseudaplodon asiatica Miller, 1927, Paleo. Sinica, Vol. 5, F. 2, pp. 5–20.
Aplodontia asiatica Friant, 1937, Ann. Mag. Nat. Hist., Vol. 10, No. 19, pp. 456–562.
Pseudaplodon asiatica Miller, 1937, Ann. Mag. Nat. Hist., Vol. 10, No. 20, p. 635.

Schlosser (1924) described an aplodontid from the Ertemte and Olan Chorea localities in Asia. He assigned the new species to the North American genus of living mountain

beavers, *Aplodontia*. Soon afterward Miller (1927) maintained that this was not assignable to *Aplodontia* and not an aplodontid and erected the genus *Pseudaplodon* to receive it. Wilson (1937) showed conclusively that the objections presented by Miller to the assignment of this species to the aplodontidae were largely invalid. Gazin (1932) and Friant (1937) reassigned the species to *Aplodontia* and the aplondontidae. In reply to Friant, Miller (1937) repeated that he did not consider the asiatic material to represent *Aplodontia*. He did not however repeat his conclusion that it was not an aplodontid. Friant (1939), in reply to Miller, repeated her position. Evidence cited elsewhere in the present study makes it obvious that when the known aplodontid material is studied there is nothing that would lead to a conclusion that the asiatic species represents *Aplodontia* or is directly related to it. However *P. asiatica* is an aplodontid as well demonstrated by a number of workers. The generic name *Pseudaplodon* is then the proper name unfortunate as it may be.

The occurrence of this material has been reviewed by numerous workers but only Friant has considered the fact that the teeth are rooted to be of any importance or even important enough to mention. Although rooted aplodontids are now known from the early Pliocene of North America they have progressed much farther than *P. asiatica,* which is geologically younger, in the development of high crowned teeth. The most important thing to the present author in the comparison of the North American and Asian rooted Pliocene aplodontids is the low crowned well rooted nature of the teeth of the asiatic form. This suggests that the asiatic form must be derived from an early form in the rooted aplodontids and is not an extension of the sequence of those presently known from North America of the later Miocene and early Pliocene.

Interrelationships of Middle and Late Cenozoic Aplodontids

Aplodontids are diversified in the early Miocene into at least four genera, *Allomys, Haplomys, Meniscomys,* and *Sewelleladon*. *Allomys,* typified by very complicated dental pattern (see fig. 6C), and *Haplomys,* a low crowned form, are evidently not directly involved in the later development of aplodontids and so will not be considered further. The diversity of aplodontids probably stems from the later Oligocene judging from the degree of divergence seen between the various genera of the John Day Formation of Oregon. *Meniscomys* which is mentioned above, mylagaulid-like in characteristics, is close if not directly ancestral to that later Tertiary family. *Sewelleladon* on the other hand is definitely an aplodontid and displays many characteristics seen in later members of the family. Both genera have the beginnings of high crowned teeth so prominent in the later development of their respective families. No record is available of Hemingfordian (mid-Miocene) aplodontids. By the Barstovian (later Miocene) they are diversified into at least two and probably three phyletic lines. The development of hypsodonty in these lines is illustrated in figure 18.

The best known line of these later aplodontids is that represented by *Liodontia* and *Aplodontia*. The Barstovian *Liodontia alexandrae* exhibits teeth with partially closed pulp cavities but not real roots. *Liodontia furlongi* of the Hemphillian has progressed to the point of persistent growth teeth as seen in *Aplodontia*. *Liodontia furlongi* presents a probable ancestor to the living mountain beaver. It differs from *Aplodontia* in the absence of mesostyles on the lower cheek teeth. Earlier workers Furlong (1910) and Taylor (1918) considered *Liodontia* to be a direct ancestor to *Aplodontia*. Wilson (1937) and McGrew (1941) suggest that this cannot be the case. They feel that the protoconid and protoflexid are too greatly reduced in *L. furlongi* to allow it to be directly ancestral to *Aplodontia*. However, the intensity of the protoflexid fold varies with the age of the individual. In young individuals the fold is the deepest whereas in older ones the protoflexid is shallow. Comparison of *Liodontia* and *Aplodontia* at approximately the same stages of wear shows the protoflexid fold of *L. furlongi* to actually be deeper than that of *Aplodontia* (figs. 3C, 4E, 3B, 4D), thus presenting no difficulty to a direct ancestral relationship between the two on this basis. Fea-

tures of the mandible and what is known of the skull of *Liodontia* do not present any serious problem to this conclusion.

A second line of aplodontids first seen in the Barstovian are those with well developed roots but developing towards high crowned teeth. In general they do not seem to have the degree of development of the masseteric crest seen in the *Liodontia-Aplodontia* line. These are the forms described above in the genus *Tardontia.*

Pseudaplodon asiatica characterized by low crowned rooted teeth is younger than any of the known *Tardontia* material but yet has not progressed much beyond the stage of development seen in *Sewelleladon.* It most probably will be seen to represent a third line of development not yet found in North America.

Mylagaulidae

Progressive changes in the occlusal pattern of the premolars of mylagaulids are of particular interest in the study of this family. The premolars are represented by five measurements each; the greatest antero-posterior distance of the tooth, the antero-posterior length of the occlusal surface, the greatest transverse measurement, the transverse width of the occlusal surface and the height of crown (total length of the tooth column perpendicular to the occlusal surface). The shape and size of the occlusal surface changes with wear in mylagaulids and thus is not useable as a comparative measurement but is useful in demonstrating wear stages. The greatest measurements are used as a basis for size comparisons. Terminology of lakes and enamel folds are similar to those employed by Cook and Gregory (1941). Additional terms include the stria-striid which are used to denote the grooves on the surface of the enamel of the column of the tooth. They are prefixed appropriately to indicate their position relative to flexures of the enamel, i.e., protostria, hypostriid, etc.

Fig. 6. A. Right lower jaw of *Allomys,* UC1444, × 2. B. Left lower jaw of *Meniscomys,* UC, × 3. C. Occlusal pattern of *Allomys,* same specimen as A, × 10. D. Occlusal pattern *Meniscomys,* same specimen as B, × 5.

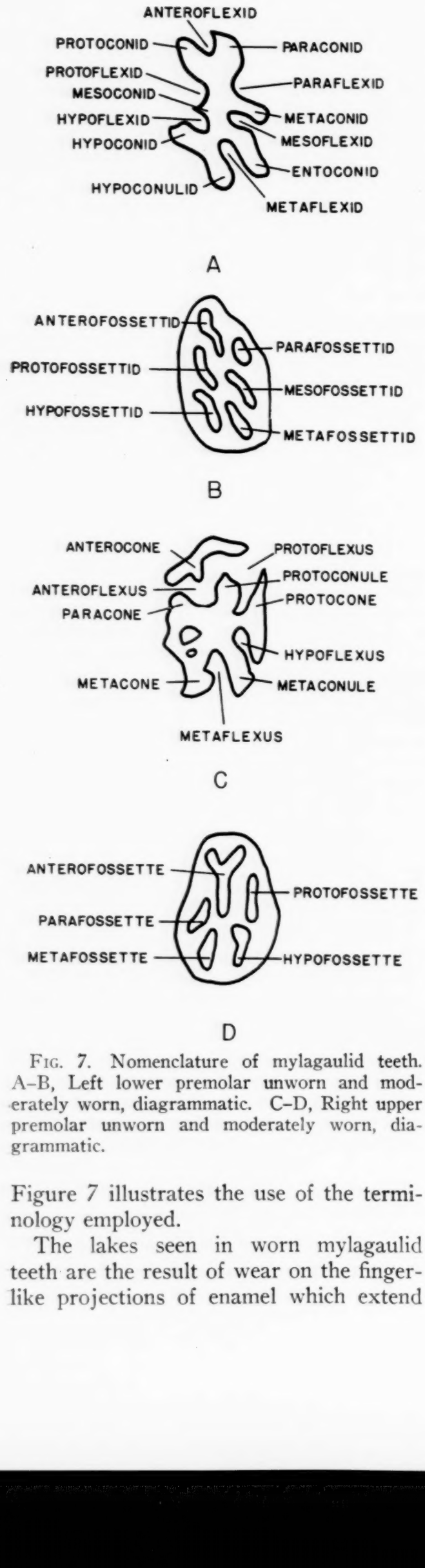


FIG. 7. Nomenclature of mylagaulid teeth. A–B, Left lower premolar unworn and moderately worn, diagrammatic. C–D, Right upper premolar unworn and moderately worn, diagrammatic.

Figure 7 illustrates the use of the terminology employed.

The lakes seen in worn mylagaulid teeth are the result of wear on the finger-like projections of enamel which extend nearly to the base of the tooth. In the unworn tooth the enamel of these fingers is contiguous with that of the outside of the tooth. Figure 8 illustrates diagrammatically the relationships of the various tooth materials and parts in unworn and worn teeth and also relates isolated lakes into their relative position in the unworn tooth. In the aplodontids the lakes or fossettes do not extend to the base of the tooth of the later Cenozoic high crowned forms but remain much the same depth as they were in earlier low crowned genera.

Description of Northern Great Basin Mylagaulids

Arikareean

John Day

Meniscomys hippodus Cope, 1878, Bull. U. S. Geol. & Geog. Surv. Terr. Vol. 4, pp. 379–396.

Meniscomys although usually classified as an aplodontid exhibits many characteristics seen in mylagaulids and as mentioned earlier might well be classified in the mylagaulidae. It seems more logical for the purposes of this study to include a description of its salient characteristics here. The fourth premolars are of particular interest because of their importance in more advanced mylagaulids. The lower fourth

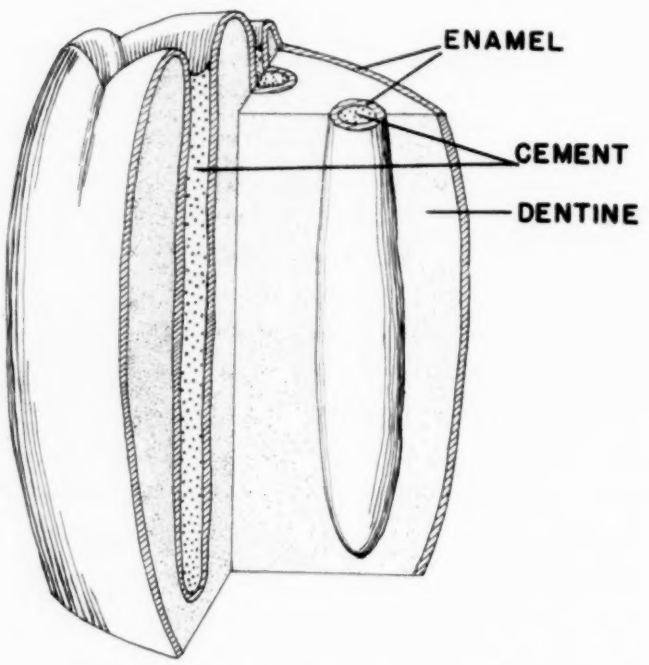


FIG. 8. Diagrammatic illustration of distribution of tooth materials in a typical mylagaulid tooth unworn and partially worn.

premolar exhibits an antereoflexid which closes to a lake with wear, proto and hypoflexids with a common external opening, and a metaflexid. The hypoflexid closes early in wear producing a hypofossettid. The protoflexid remains open apparently never closing. The metaflexid closes early in wear leaving the metafossettid. The mesoflexid apparently does not close off to form a lake until extreme wear. The paraflexid is distinct in the little worn tooth but soon is eliminated by wear. (See fig. 9A-9B.) In a little worn specimen there is an incipient anteroconid closing off the anteroflexid about halfway down the crown of the tooth. There is also a very small conulid on the anterior face of the paraconid. These two cusps are important in later mylagaulids but appear only as variations in the ancestral *Meniscomys*.

The worn lower fourth premolar of *Meniscomys* exhibits a single lake in the trigonid (anterofossettid) and two and possibly three in extreme wear in the talonid (metafossettid and hypofossettid with a possible mesofossettid). From this basic pattern the mylagaulid premolar is easily derived. (See fig. 9B.)

The upper fourth premolar exhibits four fossettes. They are the anterofossette, protofossette, an L shaped fossette extending across the width of the tooth which is a coalescing of the hypofossette and parafossette, and the metafossette. The tooth is rooted and has two well developed styles on the labial side. With wear the hypofossette and parafossette separate into individual lakes. (See fig. 9C–9D.) The upper fourth premolar of *Meniscomys* thus has the basic five lake pattern of the mylagaulids.

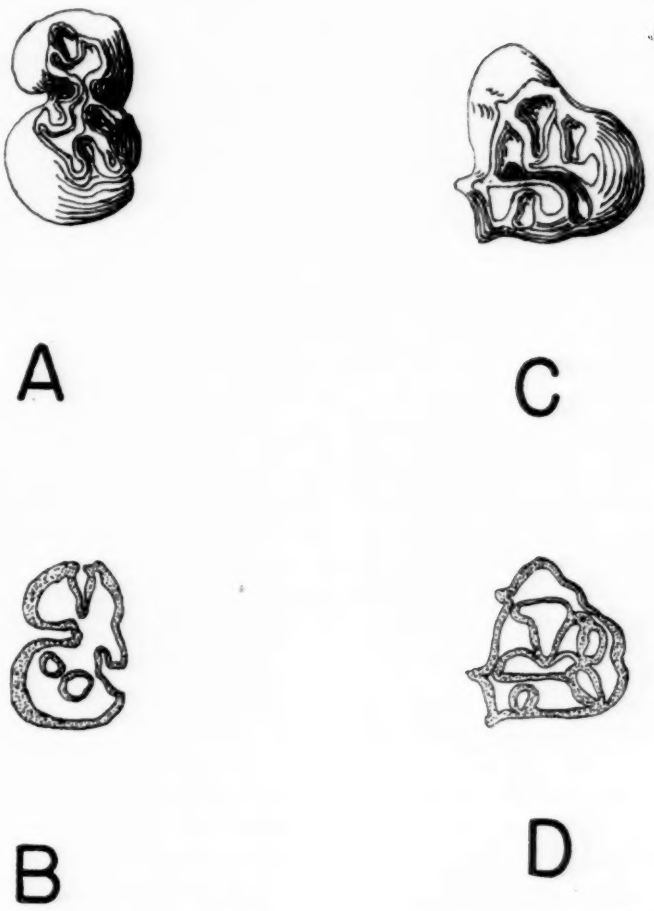


FIG. 9. Variation in occlusal pattern of fourth premolars of *Meniscomys*. A–B, Left lower P4 illustrating changes in pattern due to wear. × 5. C–D, Right upper P4 illustrating changes in pattern due to wear. × 5.

Mylagaulodon angulatus Sinclair, W. S., Amer. Jour. Sci., (4), 15, pp. 143–144.

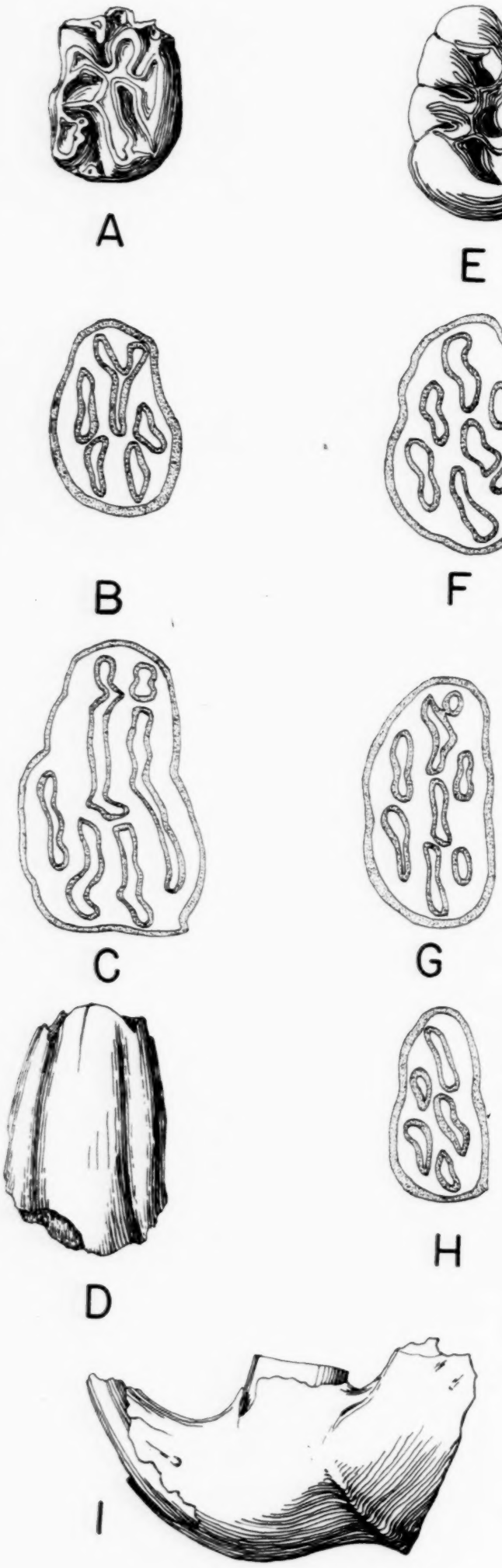
Mylagaulodon is known from the upper John Day. It is much larger than *Meniscomys* and apparently higher crowned. The anterofossette is broadened anteriorly but not Y shaped as in later mylagaulids. Little is known of this rodent. Known material is very poor. A specimen from the upper Rosebud of South Dakota has been referred to *M. angulatus* by McGrew (1941). It displays the Y shaped anterofossette. The affinities of *Mylagaulodon* to either aplodontids or mylagaulids have been discussed by earlier workers. The prominent styles are suggestive of aplodontids, but the arrangement of lakes is like that in the mylagaulids.

McGrew (1941) and Wilson (1949A) have each quoted Gazin to the effect that the type specimen of *Mylagaulodon* did not come from the John Day Formation but later beds. The locality from which the type was collected by Merriam in 1899 is UC 863. It is described as "uppermost John Day exposures near Johnson's house on South Fork of the John Day above junction of South and North Forks west side of the river." This is southwest of the present town of Kimberly, Oregon. Sinclair (1903) refers to the locality as "uppermost beds of Upper John Day, Johnson Creek." Johnson Creek is a small creek which enters the John Day River to the North. The exposures which are low topographically are capped with over a thousand feet of Columbia River Basalt. An early list of the mammals collected at the same locality and at the same time includes, *Diceratherium, Miohippus, Eporeodon, ?Agriochoerus* and *Paratylopus*. The stratigraphic position, lithology and associated fauna all indicate that this locality is in the John Day Formation. The topography makes it highly unlikely that later sediments might have contributed to the locality. The nearest known post Columbia River Basalt sediments are about twenty miles away.

Barstovian

Virgin Valley

Mesogaulus cf. *pristinis* Kellogg, 1910, Univ. Calif. Pub. Geol., Vol. 5, No. 29, p. 429.



This is apparently the only known occurrence of this genus in the Great Basin. The lack of Hemingfordian faunas in which *Mesogaulus* is more common accounts for this. The Virgin Valley material exhibits only five lakes. They lack the parafossettid. In one of the specimens which is unworn there is a small depression in the position of the parafossettid which may represent an incipient lake at that point. These specimens are much smaller than any of the other Barstovian mylagaulids seen. They have hypostriid and a thin coating of cement. (See fig. 10H.)

Mylagaulus cf. *laevis* Kellogg, 1910, Univ. Calif. Pub. Geol., Vol. 5, No. 29, p. 429.

The basic pattern of the lower premolar consists of six lakes. These are the proto, hypo, meso, meta, para and anterofossettids. Both hypo and protostriids are present and sometimes very prominent (fig. 10, E, F, G).

Typically there are five lakes in the upper premolar. They are proto, hypo, antero, para and metafossettes. In some instances there is a small additional lake just posterior to the parafossette. Lakes of joint para-metafossette origin are common in later mylagaulids but only appear as variants in the Virgin Valley material. The hypo and proto striae are present and prominent as in the lowers. There is also a prominent groove down the anterior face of the tooth (fig. 10A, B, C, D).

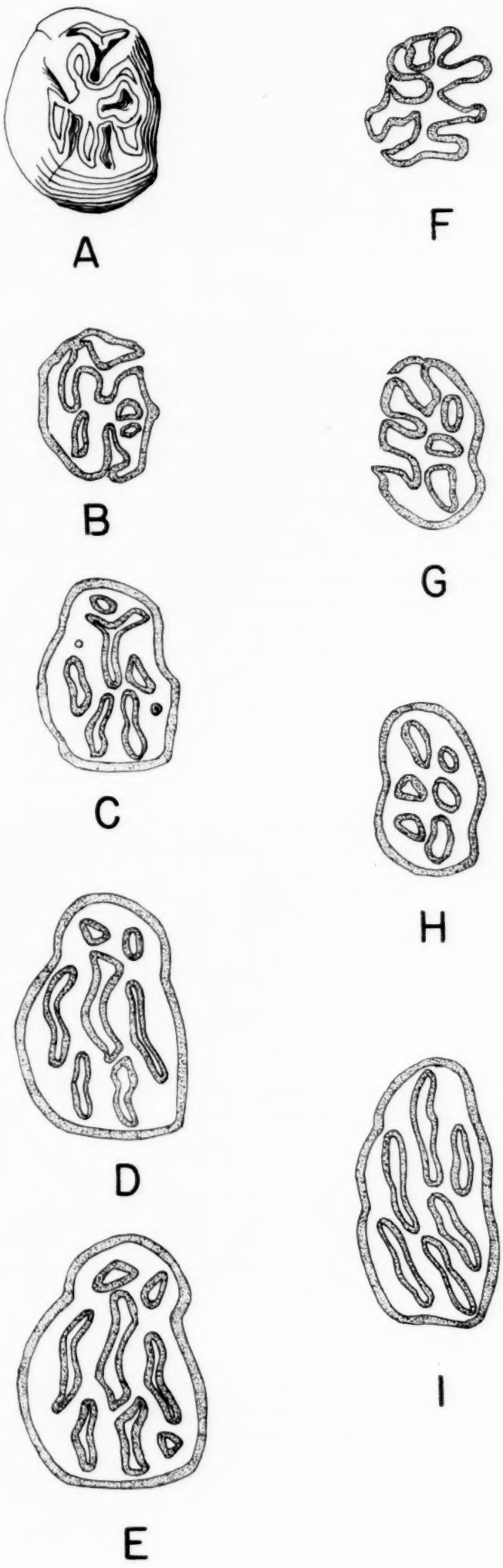
Paulina Creek

Mylagaulus sp. Downs, T., 1956, Univ. Calif. Pub. Geol. Sci., Vol. 31, No. 5, p. 214.

Paulina Creek is a locality in the Crooked River drainage south of the type Mascall locality. Seven specimens were available from this locality in the Y. P. M. and UOMNH collections.

Lower premolars are very similar to the Virgin Valley *Mylagaulus*. Parafossettid does not persist with wear and in one instance there is an additional mesofossettid. Proto and hypostriids are prominent. Well worn teeth are rooted.

FIG. 10. Virgin Valley, Nevada, mylagaulids illustrating variations of wear and some individual variation. A–C, Upper fourth premolars illustrating variations in occlusal pattern due to wear, UC11633, UC41025, CIT, UC40955, × 2.5. D, Labial view of upper fourth premolar illustrating the development of Hypo and Protostria, UC40955, × 2.5. E–G, Lower left fourth premolars illustrating variation in occlusal pattern due to wear, UC11633, UC11572, UC41026, × 2.5. H, Lower left fourth premolar of *Mesogaulus,* UC11843, × 2.5. I, Left lower jaw, UC41026, × 1.



The basic five lake pattern is typical in the upper premolars. In one specimen there is an additional metafossette. There is a strong protostria. In all characteristics studied these specimens are close to the Virgin Valley material, probably conspecific.

Beatty Butte

Mylagaulus cf. *laevis* Wallace, R. E., 1946, Carn. Inst. Wash. Pub. 551, p. 124.

Basic pattern of the lower premolar consists of the six lakes from the six flexids. In little worn material the lakes are directed somewhat transversely but in well worn material the lakes are shifted around to nearly an antero-posterior direction. In one specimen there is an additional lake which is apparently derived from the metafossettid. The parafossettid is quite small in little worn specimens but becomes longer with wear. It is present in all the material seen. The hypostriid is prominent. Cement is present on the teeth. A typical wear series is illustrated (fig. 11, G, H, I).

Five lakes are present in little worn upper premolars. In addition to these there is a small lake just posterior to the parafossette similar to that seen in the Virgin Valley material. The persistency of this lake varies greatly. The anteroflexid which is Y shaped on wear breaks into three separate lakes. The two arms of the Y isolate one at a time to form two small lakes while the base of the Y becomes a rather long antero-posteriorly directed lake. This breaking down of the Y shaped anterofossette with wear is apparently typical of most *Mylagaulus* material studied. A typical wear series is illustrated (fig. 11 A–E).

The material from Beatty Butte differs from the previously described specimens in a number of characteristics. The parafossettid is more persistent in the Beatty Butte mylagaulid, apparently not being removed with wear as in the Virgin Valley and Paulina Creek material. The protostria and protostriid are not prominent and usually not recognizable whereas they play a prominent part in the general appearance of the Virgin Valley and Paulina Creek material. The materials of the three localities mentioned above are similar in the occasional appearance of additional metafossettid and parafossette lakes.

Sucker Creek

Mylagaulus cf. *laevis* Scharf, D. W., 1935, Carn. Inst. Wash. Pub. 453, p. 104.

FIG. 11. Beatty Butte, Oregon, mylagaulids illustrating variations in occlusal pattern due to wear and individual variation. A–E, Upper left fourth premolars, CIT, × 2.5. F–I, Lower left fourth premolars, CIT, × 2.5.

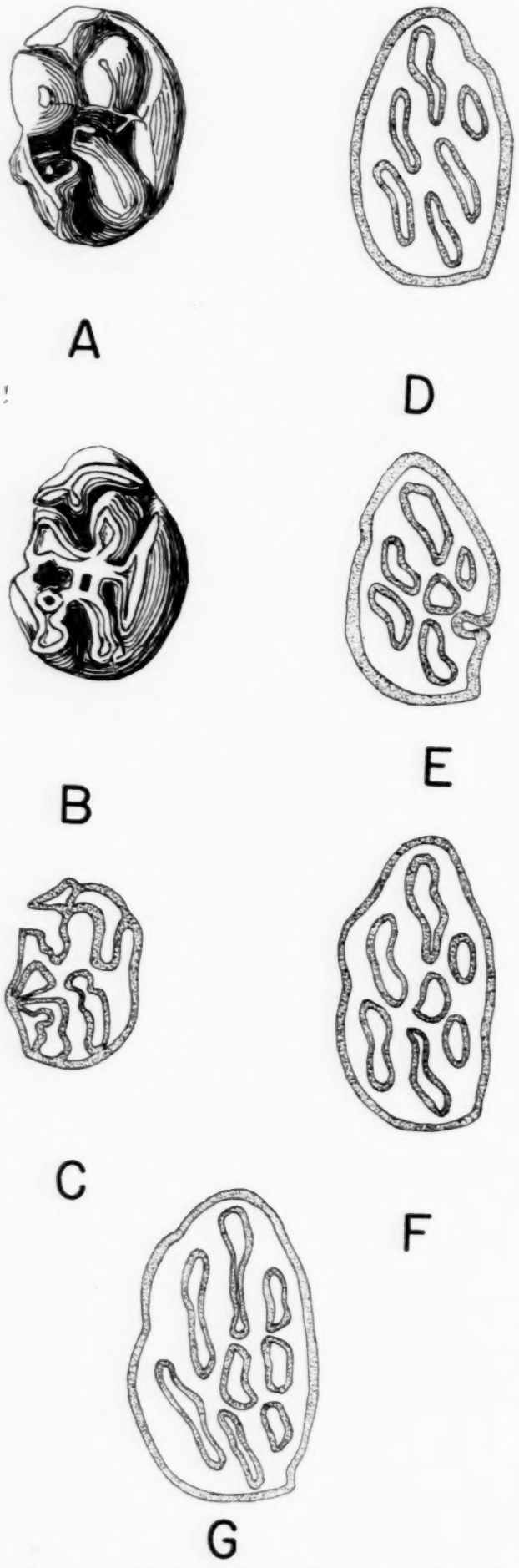


FIG. 12. Skull Springs, Oregon, mylagaulids illustrating variations in occlusal pattern due to wear and individual variation. A–C, Upper right fourth premolars, CIT, × 2.5. D–G, Lower left fourth premolars, CIT, × 2.5.

A single upper premolar in the CIT collection represents *Mylagaulus* in the Sucker Creek fauna. The antero, proto and hypofossettes are similar to those of material already described. The meta and parafossettes however, are connected at the stage of wear seen. This is not uncommon in later mylagaulids and may continue into the well worn tooth. There is also an additional small lake just lingual to the metafossette and probably derived from it.

Skull Springs

Mylagaulus cf. *laevis* Gazin, C. L., 1932, Carn. Inst. Wash. Pub. 418, p. 69.

Additional meso or parafossettids are present in all but one lower premolar studied. The parafossettid is larger than in the Beatty Butte material and the roots do not become so well developed. Striids are not present. Variations illustrated (fig. 12 D, E, F, G).

None of the upper premolars seen had less than six lakes. Five of the lakes were those seen in the other material described above. The sixth lake is a small one derived from the hypofossette. In the unworn tooth the protoconule does not directly meet the edge of the tooth, as in the Beatty Butte material, for instance, but is separated by a well developed cingulum. The presence of this cingulum and the depression between it and the protoconule results in a more persistant connection between the anteroflexid and protoflexid in early wear. In unworn material there is a small fold in the anterior face of the upper premolar anterior to the anteroflexid which does not appear at any time in the occlusal pattern. This small fold however, is seen in Clarendonian mylagaulids as a new lake (Antifossette) between the arms of the Y shaped anterofossette in moderate wear (fig. 12, A, B, C).

Clarendonian

Clarendonian mylagaulids have only recently been discovered in the Northern Great Basin.

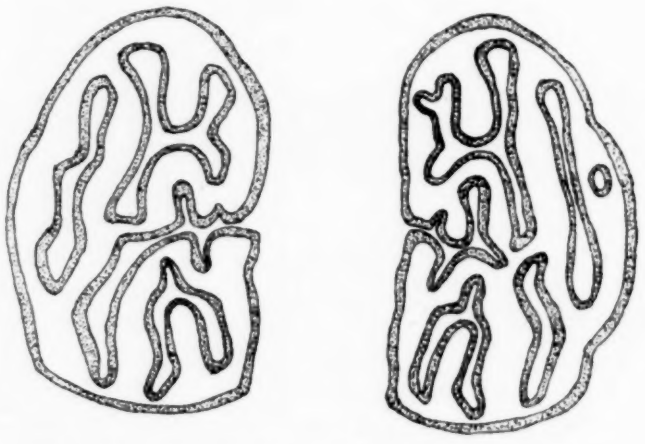


FIG. 13. *Epigaulus minor,* upper fourth premolars, left and right, from Juntura, Oregon, UOMNH F-6165, F6166, × 4.

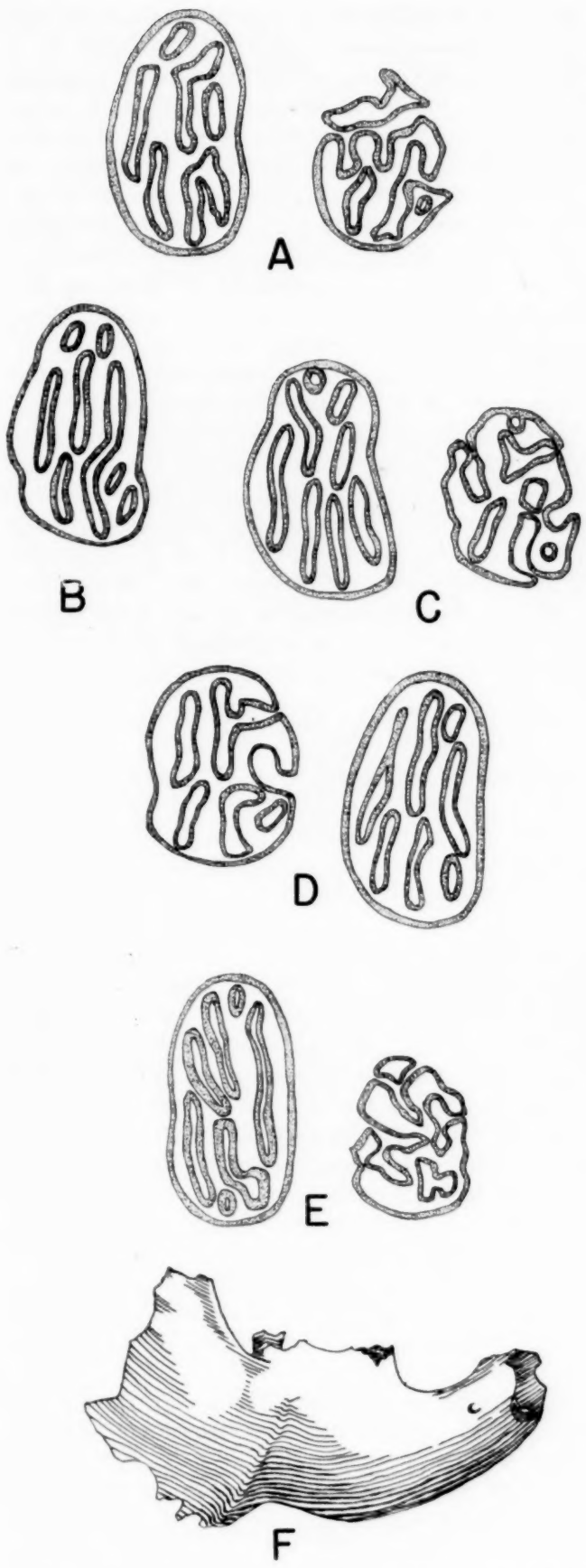


FIG. 14. Juntura, Oregon, mylagaulid illustrating variations in occlusal pattern. A. Upper left fourth premolar, unworn and worn pattern from sectioned specimen, UOMNH F5425, × 2.5. B. Upper left fourth premolar well worn, UOMNH F5443, × 2.5. C. Upper left fourth premolar unworn and worn pattern from sectioned specimen, UOMNH F5558, × 2.5. D. Upper left fourth premolar unworn and worn pattern from sectioned specimen, UOMNH F5557, × 2.5. E. Lower left fourth premolar unworn and worn pattern from sectioned specimen, UOMNH F6273, × 2.5. F. Lower right jaw, UOMNH F5770, × 1.

Parties from the University of Oregon Museum of Natural History have collected several faunas in northern Malheur and Harney counties of southeast Oregon which include a number of mylagaulids. A single mylagaulid tooth is known from the Brady Pocket Nevada locality. These faunas are described elsewhere.

Juntura

Epigaulus minor Hibbard, C. W., and L. F. Phillis, 1945, Bull. Univ. Kansas, Vol. 30, pt. 2, p. 551.

Two upper fourth premolars of opposite sides were collected within a few inches of each other as float. No other specimens referable to *Epigaulus* were collected (UO Loc 2343) (fig. 13).

Mylagaulus sp.

The lower premolar exhibits seven lakes. Although this number of lakes has been described above in other mylagaulids those found in the Juntura material are of different derivation. Mesoflexid and paraflexid may have a common external opening in little worn teeth. The resultant fossettids are also joined and form a long single para-mesofossettid. These are separate in the material thus far reviewed. The anterofossettid is Y shaped much as in the upper premolars because of the increased development of the anteroconid. The lingual branch of the Y isolates to leave a small round lake which persists into moderate wear. The labial branch and stem of the Y straighten to form a single long lake with wear. The proto and hypoflexids are joined in early wear with a common external opening. They are, however, separated with wear. The metafossettid is pinched in early wear similar to a specimen from Virgin Valley and separated into two lakes with wear. The size of the additional lake varies (fig. 14E).

Moderately worn upper premolars from Juntura exhibit six lakes. This is a number similar to other mylagaulids noted above but as in the case of the lowers the lakes in the Juntura material are of somewhat different derivation. The anterofossette is Y shaped and breaks into three separate lakes in extreme wear as was seen in the Barstovian species described above. In early to moderate wear there is a small lake which appears between and anterior to the two arms of the Y of the anterofossette. This lake is derived from an infolding of the enamel of the anterior face of the tooth. Not all specimens have this lake.

Early development of this lake can be seen in a small fold on the anteroconid of unworn material from Skull Springs. This new flexid is referred to here as the antiflexid. The para and meta fossettes are commonly but not always connected. The meta and parafossette may be completely fused to form a long somewhat diagonally oriented lake with two metafossette lakes labial to it (fig. 14B), or, in other instances, a portion of this fused metaparafossette is isolated anteriorly and the remaining portion is recurved posteriorly following the original position of the paraflexid. (Fig. 14C). In material in which the para and metafossettes are not fused the metaflexid produced two small lakes and the paraflexid wears one or two lakes. When only one parafossette is formed it is usually a long lake (fig. 14).

Hemphillian

Rome

Mylagaulus cf. *monodon* Wilson, R. W., 1937, Carn. Inst. Wash. Pub. 487, p. 6.

Moderately worn lower premolars have eight to nine lakes. The labial branch of the Y shaped anteroflexid is weak and does not enter into the lake pattern after partial wearing of the tooth. The lingual branch which remains connected to the stem of the Y after the labial branch separates is isolated by continued wear and results in two anterofossettes. This is similar to the wear changes in the Juntura species but the lingual anterofossette is much larger. In little worn material the metaconid is isolated by the juncture of the meso and paraflexids. With wear they become separate fossettids. The mesofossettid divides with wear to produce two lakes usually side by side. The metafossettid rarely produces a small lake lingual to the larger metafossettid but it does not last beyond moderate wear. See illustrations of variations and wear series (fig. 15D–G).

As in the Juntura species the upper premolars have a small flexus between the arms of the Y of the anterofossette which forms a small lake with wear, the antifossette. This lake does not ordinarily last past the little worn stage but on occasion may last into moderate wear. The anterofossette divides with wear into two lakes, a long one representing the lingual arm and stem of the original Y and a short one derived from the labial branch of the Y. Apparently there is no further division of the fossette into a third lake as is so common in the other materials reviewed above. The meta and parafossette are joined in some cases to produce a long diagonally oriented lake in later wear. However in most of the material they are separated or become separated in early wear. The parafossette often has one small additional labial lake in addition to the larger one. On occasion the posterior ends of the two parafossettes remain connected resulting in a hooked parafossette. This may be a common occurrence and represent a stage of wear prior to the separation of the two lakes (fig. 15A–C).

The Rome material exhibits a number of characteristics seen in the Juntura material; the common fusion of para and meta fossettes, the production of several additional metafossettes, the usual appearance of at least one additional parafossette, the appearance of a small short lived lake between the arms of the Y and anterofossette (the antifossette), the development of a Y shaped anterofossettid and the division of this fossettid into two lakes upon wear. The Rome material while it resembles the Juntura species in these characters, has them developed to a much greater extent and is much larger than the Juntura material. Their differences and similarities appear to be those involved in a simply phylogenetic step. Their stratigraphic difference in age further suggests that this is the case.

McKay Reservoir

Mylagaulus sp. Shotwell, J. A., 1955, Bull. G. S. A., Vol. 67, p. 727.

Since the original description of the McKay Reservoir fauna more material has been found.

The lower premolar is equal in size to the specimen from Thousand Creek. They have 9–10 lakes in the wear stages studied (2 well worn specimens). The material available does not allow direct interpretation of the origin of the lakes but comparisons with the Rome specimens indicates the following. Antifossettid is not present in the well worn material. The anterofossettid breaks down to two lakes with wear. Para and meso fossettids join and also produce an extra lake apiece. The metafossette has an extra lake. A small lake on one of the specimens between the para and anterofossettids may be derived from the anterofossettid. The combined para-mesofossettid is S shaped and similar to that of the Rome species (fig. 15K–L).

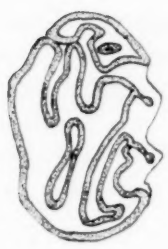
The single upper premolar known exhibits nine lakes. Two anterofossettes, one protofossette, one hypofossette, two metafossettes and three parafossettes, one quite small. This is also similar to the Rome species (fig. 15J).

Developmental Trends as Exhibited by the Fourth Premolars

Variation in Origin and Number of Lakes

Lower premolars

Table 1 summarizes the variation in number and origin of lakes in the lower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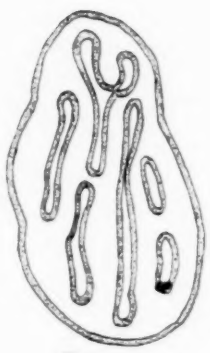
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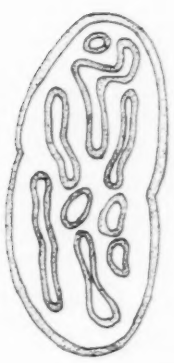
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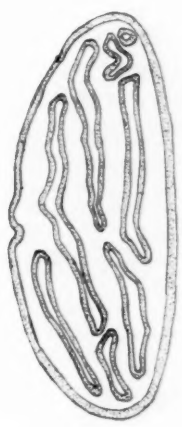
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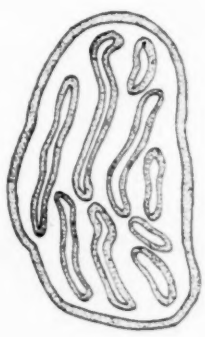
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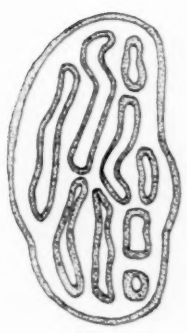
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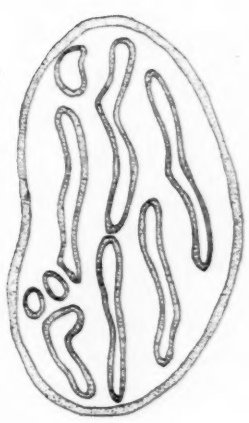
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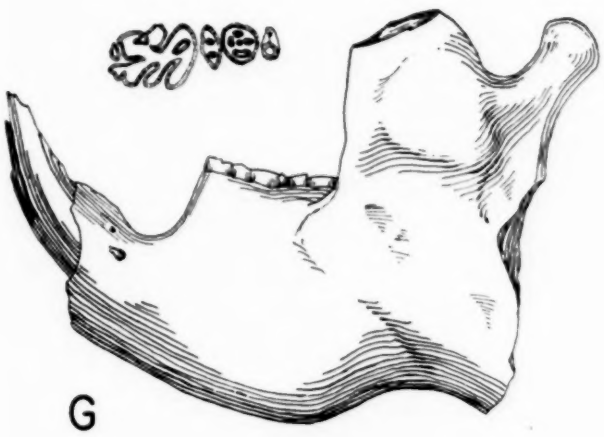
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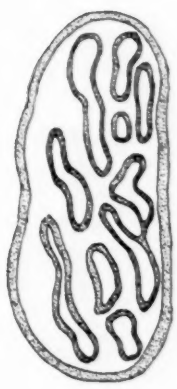
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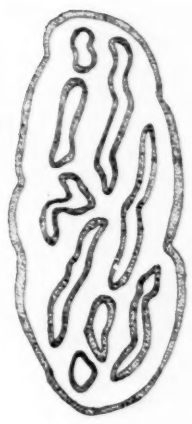

L

FIG. 15. Hemphillian mylagaulids. Rome, Oregon. A–C. Wear series in upper left fourth premolars, CIT, × 2.5. D–F. Wear series in lower left fourth premolars, CIT × 2.5. G. Left lower jaw and little worn dentition, CIT, × 2.5. Thousand Creek, Nevada. H. Upper fourth premolar, UC11878, × 2.5. I. Lower fourth premolar, CIT, × 2.5. McKay Reservoir, Oregon. J. Upper fourth premolar, UOMNH, × 2.5. K–L. Lower fourth premolars, UOMNH, × 2.5.

TABLE 1. *Variation in number and origin of lakes in the lower fourth premolar of Great Basin mylagaulids.* Range of total numbers of lakes includes variations due to wear and individual differences. These are ranges of numbers of lakes which occur at any one time in wear in any single individual.

Provincial Age	Barstovian				Clar.	Hemphillian		
Lake \ Fauna	Virgin Valley	Paulina Creek	Beatty Butte	Skull Springs	Juntura	Rome	Thousand Creek	McKay Reservoir
Antifossettid						0–1	1	?
Anterofossettid	1	1	1	1	1–2	1–2	2	2–3
Protofossettid	1	1	1	1	1	1	1	1
Hypofossettid	1	1	1	1	1	1	1	1
Parafossettid	0–1	0–1	1	1	½–1	½–1	1	1½
Mesofossettid	1	1	1	1–2	½–1	1–1½–2	1	1½
Metafossettid	1	1	1	1–2	1–2	1–2	1	2
Range	5–6	5–6	6	6–8	5–8	7–9	8	9–10

fourth premolar in Northern Great Basin mylagaulids. There is an increase in the number of lakes from five in the Barstovian specimens to ten in some of the Hemphillian material. However, all but one of the added lakes are derived from flexids present in *Meniscomys*. Only three of the flexids result in lakes in the fourth premolar of *Meniscomys* (ant. meta and hypo). The antiflexid which produces a small lake in Hemphillian specimens is formed by an infolding of the exterior face of the anteroconid a cusp appearing as a very small stylar cusp in *Meniscomys*. All other new lakes in later mylagaulids studied are the result of the fragmentation of the six basic flexids. Only certain flexids take part in this fragmentation. The hypo and protoflexids do not produce more than a single fossettid in the material studied. In the Barstovian materials the meso and metaflexids are the only producers of more than one lake. In the Clarendonian species the para and mesoflexids are often combined into one large lake, the metaflexid produces an extra fossettid and the anteroflexid first results in more than a single lake upon wear. In the Hemphillian species all of the former variants appear with the addition of an antifossettid from a flexure in the face of the anteroconid. Vertical ridges and small extensions of the enamel wall of flexures are often seen in Barstovian specimens which apparently develop to produce the

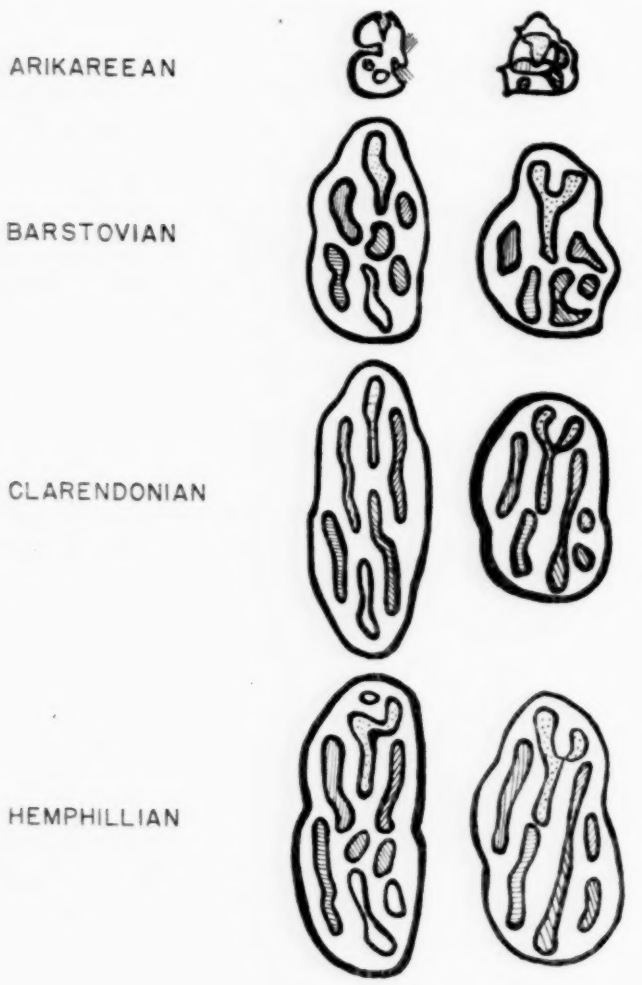


FIG. 16. Developmental sequence of occlusal pattern of fourth premolars of mylagaulid rodents in the Great Basin. Patterns indicate homologous lakes.

TABLE 2. *Variation in number and origin of lakes in the upper fourth premolar of Great Basin mylagaulids.* Range of total numbers of lakes includes variations due to wear and individual differences. These are ranges of numbers of lakes which occur at any one time in wear in any single individual.

Provincial Age	Barstovian				Clar.	Hemphillian		
Lake \ Fauna	Virgin Valley	Sucker Creek	Beatty Butte	Skull Springs	Juntura	Rome	Thousand Creek	McKay Reservoir
Antifossette					0–1	0–1	?	?
Anterofossette	1–2–3	1–3	1–3	1–3	1–3	1–2	1–2	1–2
Protofossette	1	1	1	1	1	1	½–1	1
Hypofossette	1	1	1	1	1	1	½–1	1
Metafossette	1–2	½	1	1	1½–2	1½–3	2	2
Parafossette	1–2	1½	1–2	2	1–1½–2	1–1½–2	2	3
Range	5–7	5–7	5–8	6–8	6–8	7–10	6–8(9)	9(10)

closures which result in an additional lake from a particular flexure in later mylagaulids (fig. 16).

Upper premolars

The variation in number and origin of lakes of the upper premolars are presented in table 2. As few as five lakes are noted in Barstovian materials and as many as ten in those of the Hemphillian. In Barstovian specimens the anteroflexus and paraflexus occasionally produce more than one lake. In one instance the para and metafossettes are joined. In the Clarendonian material the meta and parafossettes may join. They each also produce extra lakes. The antiflexus produces a small but not very persistent lake between the arms of the Y shaped anteroflexus. The Hemphillian material combines all these variations. As in the lower fourth premolar the proto and hypoflexi each produce a single lake in all the material seen.

Tables 1 and 2 demonstrate along with figure 16 the nature of the sequence of development of mylagaulid teeth from the Barstovian to the Hemphillian. Table 3 shows the marked increase of size of the premolars during the same period of time. There is an increase in number of lakes exposed at any one stage of wear from Barstovian to Hemphillian species. All these lakes save one arise from the same infoldings of enamel recognizeable in mylagaulids as early as the Arikareean (early Miocene). The increase in number is accomplished by fragmentating of the lakes resulting from isolated infoldings of enamel. This fragmentation does not occur in all lakes. It is almost entirely restricted to the labial side of the upper premolars and the lingual side of the lower premolars. The metafossette and parafossette on the labial side of the upper premolar show the most significant increases. Whereas the anterofossettid of the lower premolar shows the greatest increase in number of lakes produced although other fossettids also show important changes. Pliocene mylagaulids can be separated from Miocene ones by their rather consistent possession of at least one lake originating from the fusion of a portion of the metafossettid and parafossettid in lowers or the metafossette and parafossette in uppers. They also display a new lake not seen in earlier species termed the antifossette in uppers and antifossettid in lowers. The premolars of Pliocene mylagaulids are larger than those of Miocene forms reaching extremes in the Hemphillian species. There is a tendency for lakes to become greatly elongated with wear in Pliocene mylagaulids. Examination of a limited amount of Great Plains mylagaulid material from the Niobrara River, Claren-

TABLE 3. *Measurements of size differences in Great Basin mylagaulids.* PA—Posterior-anterior length, TR—Transverse diameter, HC—Height of crown of little worn teeth if present in sample. N.sp.—Number of specimens, M—Mean, SD—Standard deviation.

Lower premolar	PA			TR			HC
	N.sp.	M	SD	N.sp.	M	SD	
Virgin Valley	4	9.9	0.82	4	4.9	0.71	18.1
Beatty Butte	8	9.8	0.50	9	4.8	0.75	16.1
Skull Springs	6	9.5	0.25	6	5.0	0.55	—
Sucker Creek	1	8.5	—	1	5.5	—	—
Juntura	2	10.0	—	2	5.1	—	16.7
Rome	2	13.4	—	2	6.1	—	20.1
McKay Reservoir	1	14.1	—	1	6.7	—	—
Thousand Creek	1	14.9	—	1	6.8	—	—
Upper premolar							
Virgin Valley	6	9.1	1.35	6	5.4	1.04	17.0
Beatty Butte	7	9.3	0.22	6	6.1	0.63	19.1
Skull Springs	6	9.3	0.96	6	5.3	0.14	16.1
Juntura	5	9.8	0.43	5	5.7	0.35	16.7
Rome	3	11.8	—	3	6.3	—	20.5
McKay Reservoir	1	14.1	—	1	8.7	—	19.1
Thousand Creek	1	10.0	—	1	5.7	—	—
Bartlett Mtn.	4	11.8	1.45	4	7.3	1.00	—

don, Burge, Big Springs Canyon, Pliohippus Draw, Optima and Hemphill faunas indicates that the sequence of developmental changes seen in the Great Basin materials is the same as in the plains.

Hypsodonty and Size

Table 3 presents data on size and hypsodonty in the material studied. It is interesting to note that the Hemphillian mylagaulid skull and presumably the rest of the skeleton indicate an increase in gross size of about 45% over the Barstovian forms. The areas of occlusal surface of the premolars doubles and the length of enamel contact surface of the lakes increases by about 80% in the progression from Barstovian to Hemphillian mylagaulids. The molars change very little in size but are all gone in moderately worn Hemphillian species, though present when the premolar is little worn. The increase in actual height of crown is very slight and probably not significant after the Barstovian, in fact the Barstovian forms are relatively as high crowned (considering their smaller size) as those of the Hemphillian (fig. 17–18).

Hypsodonty in small mammals with non-ever-growing teeth can only be developed to the limit presented by the depth of the jaw in which the tooth rests. In a form which has an enlarged premolar this is even more limiting. Increased wearing volume and surface can only be had by further increase in the bulk and complexity of the enamel of the tooth. This is what happens in the forms studied. The size of the animal has increased about one-half, the area of occlusion has been doubled and the enamel surface not quite doubled. Since hypsodonty and complication of enamel pattern occur at different times in the history of these rodents it seems likely they are independent genetic traits.

Figures 19, 20, 21 illustrate the skulls of Barstovian, Clarendonian and Hemphillian mylagaulids. Good skull material is so rare that only a few characteristic changes can be noted with any

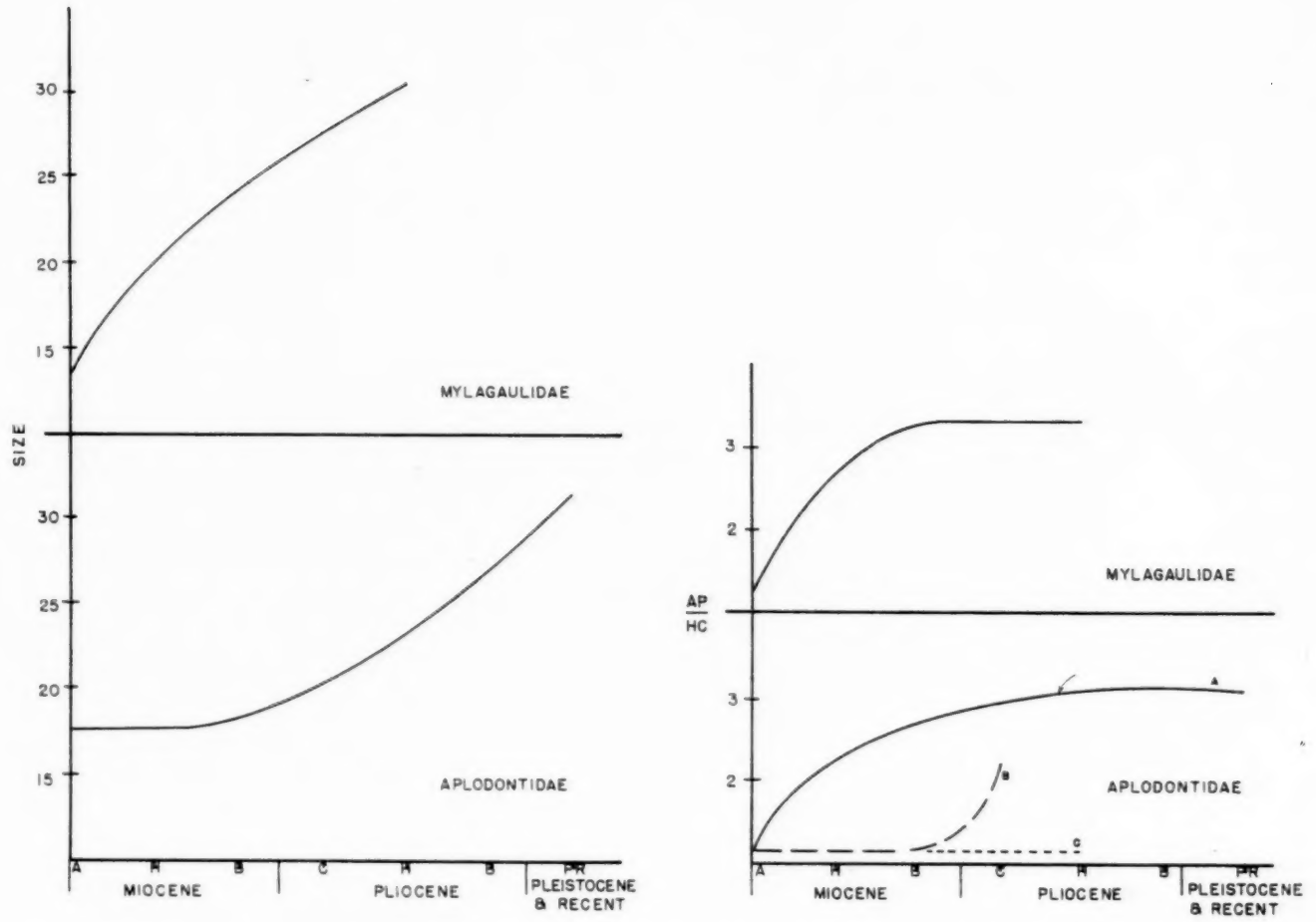


FIG. 17. Size changes in mylagaulid and aplodontid rodents as seen in linear measurements of the lower jaw. Letters indicate provincial ages.

FIG. 18. Relative hypsodonty changes in mylagaulids and aplodontids as shown in the ratio of anterior-posterior length of the tooth to the height of crown in the fourth premolar. A. *Liodontia-Aplodontia* line. B. *Tardontia*. C. *Pseudaplodon*. Arrow on A indicates point of development of persistant growth teeth.

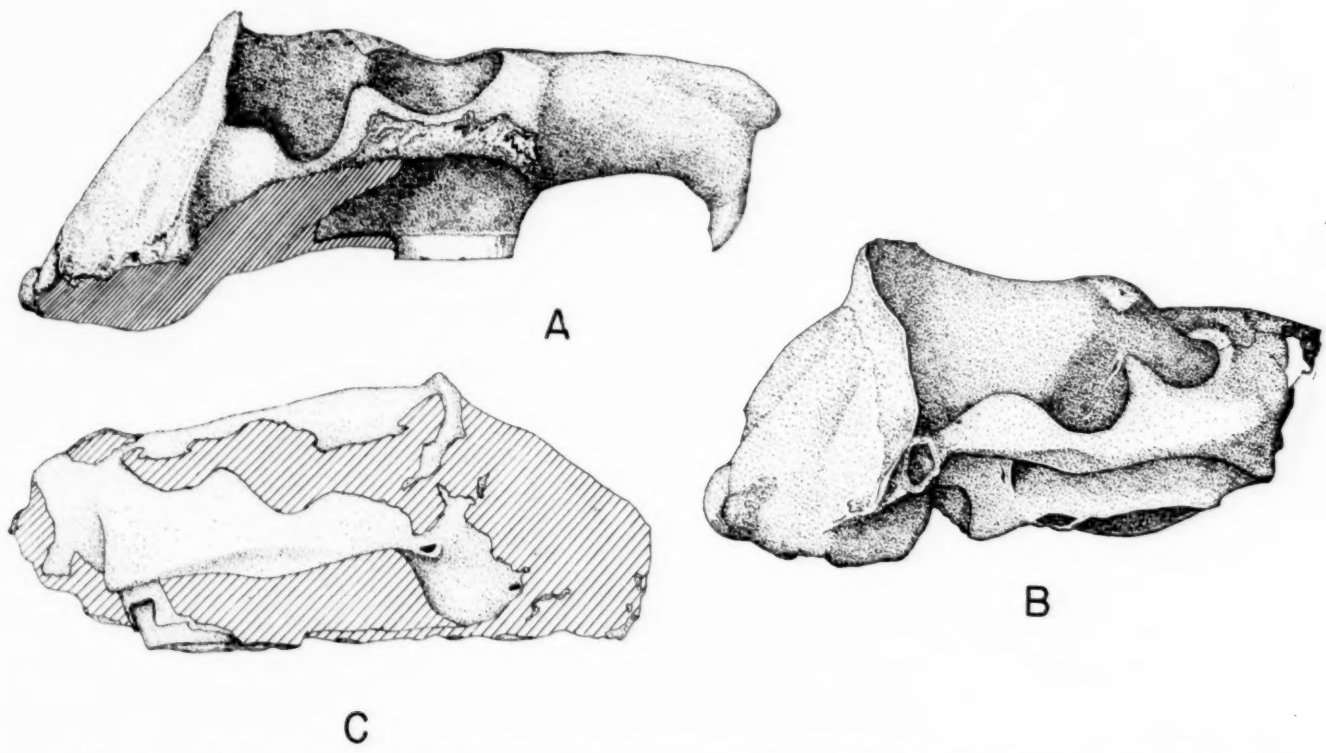
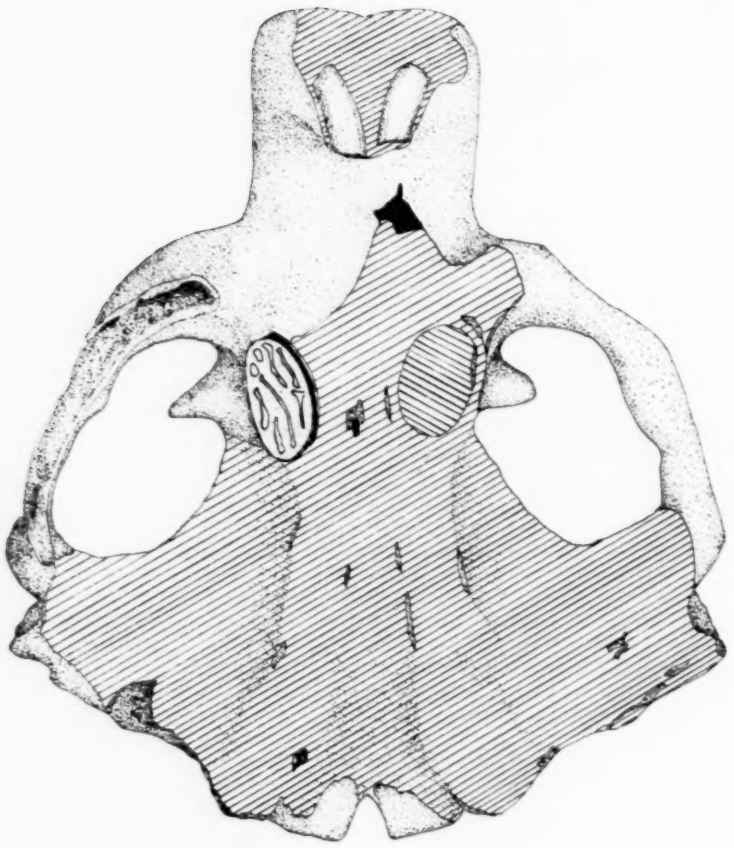


FIG. 19. Barstovian, Clarendonian, and Hemphillian mylagaulid skull sequence, side view. A. Bartlett Mountain, Oregon, Hemphillian, CIT, × 1. B. Big Springs Canyon, South Dakota, Clarendonian, UC32323, × 1. C. Skull Springs, Oregon, Barstovian, CIT, × 1.



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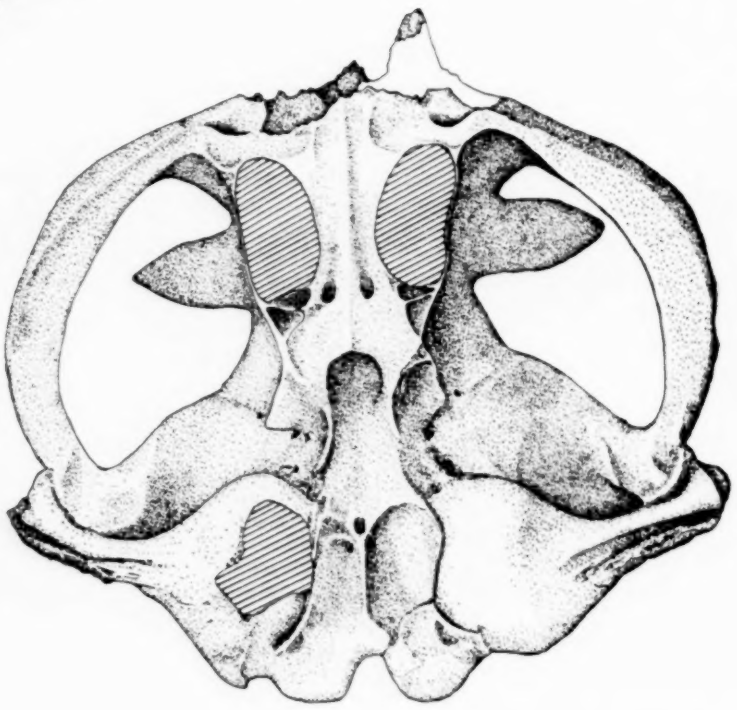

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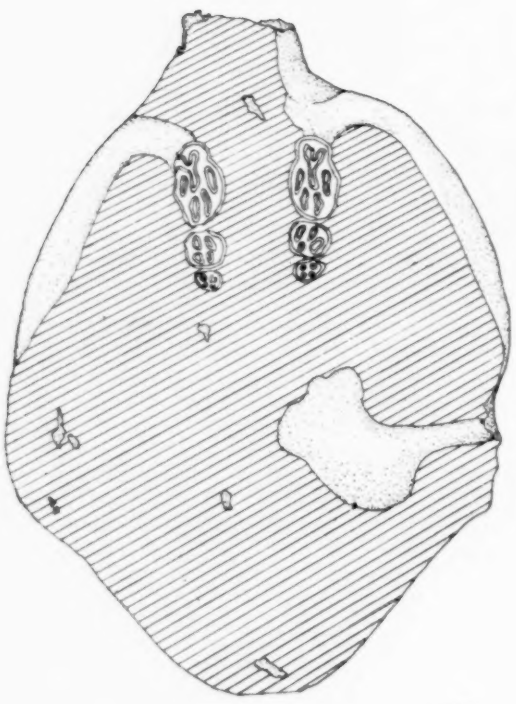

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FIG. 20. Ventral view skull sequence of figure 19.

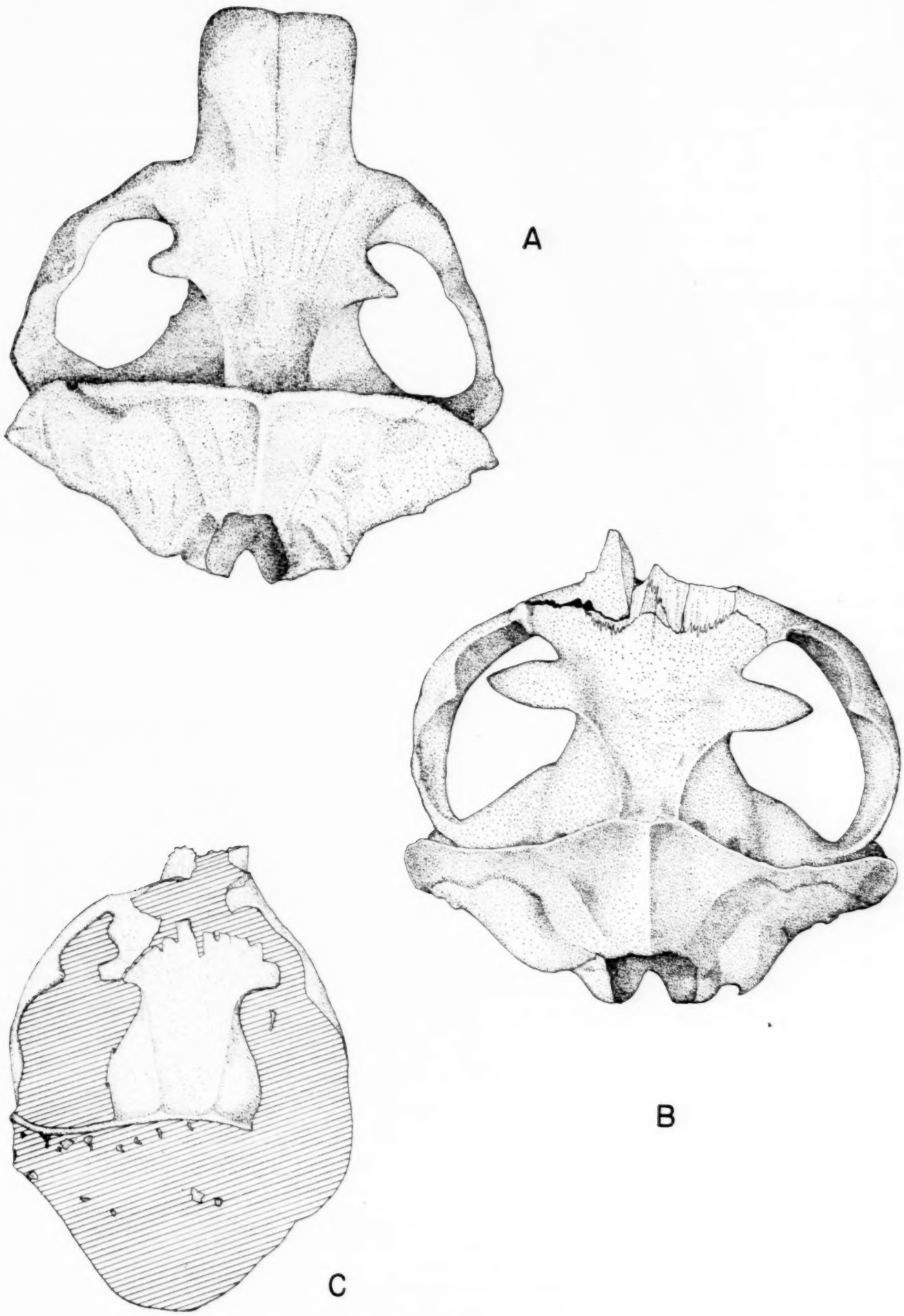
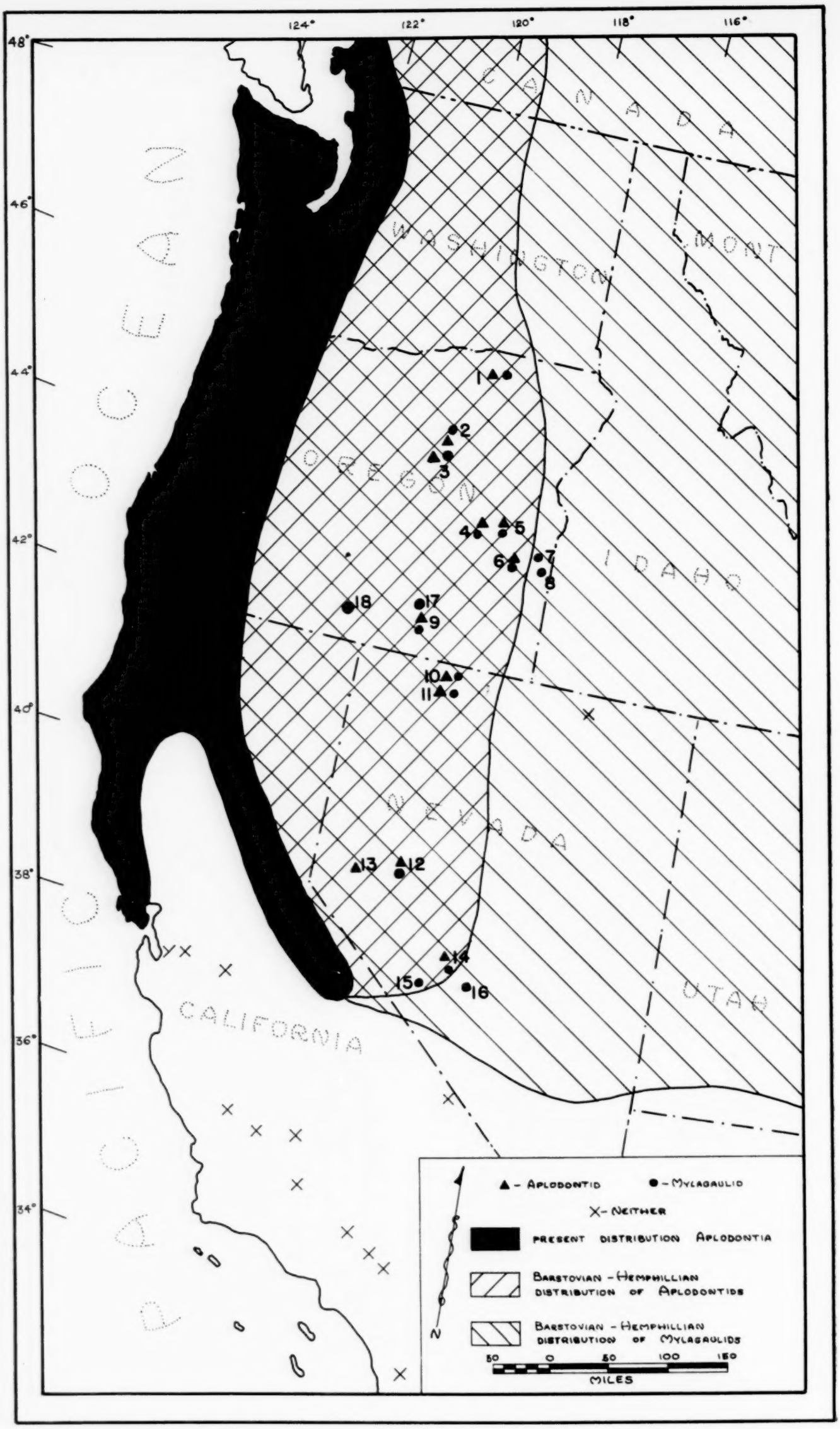


FIG. 21. Dorsal view skull sequence of figure 19.


124°
122°
120°
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48°
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PACIFIC OCEAN
CANADA
WASHINGTON
MONT.
OREGON
IDAHO
NEVADA
UTAH
CALIFORNIA
1
2
3
4
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6
7
8
9
10
11
12
13
14
15
16
17
18
▲ - APLODONTID
● - MYLAGAULID
X - NEITHER
PRESENT DISTRIBUTION APLODONTIA
BARSTOVIAN - HEMPHILLIAN DISTRIBUTION OF APLODONTIDS
BARSTOVIAN - HEMPHILLIAN DISTRIBUTION OF MYLAGAULIDS
N
50 0 50 100 150
MILES

confidence. The most obvious difference is the increase in size of the skull through this progression. Another change seen is the increase in the angle of the occiput with the horizontal plane of the skull. This is in contrast to the aplodontids in which the occiput is nearly at right angles to the horizontal plane of the skull (fig. 6A). The occipital crest of the Barstovian form has an anterior embayment at the midline of the skull. This is also seen in the Clarendonian form. However, in the Hemphillian mylagaulid illustrated the occipital crest is very nearly straight (fig. 21, A, B, C). All the specimens illustrate well developed but incomplete post orbital bars. These are not seen in the aplodontids. Both aplodontids and mylagaulids have a well ossified auditory meatus.

Historical Biogeography

With the exception of an occurrence in Asia, aplodontid and mylagaulid rodents are restricted to North America throughout their history. Figure 22 is a map of their distribution past and present in Western North America. The data from which the map is made is taken from the faunal lists of post Arikareean mammalian localities in western North America. Negative evidence from these lists is used only when the collection indicates that rodents and lagomorphs were collected but no evidence of mylagaulid or aplodontid rodents was present. The map indicates four facts concerning the distribution of these two families. They are:

1. The limits of the present distribution of *Aplodontia,* the only living representative of either family.
2. The extent of the former distribution of post Arikareean aplodontids.
3. The extent of the former distribution of post Arikareean mylagaulids.
4. The occurrence of faunas with no record of either family present.

The distribution of the living *Aplodontia* needs no explanation. The distribution of post Arikareean aplodontids is not differentiated as to particular time. There are no post-Hemphillian records known outside the present distribution of *Aplodontia.* The distribution of mylagaulids is much broader than the map indicates. They are known from the Arikareean to Hemphillian not only in the area of the map but in the great plains from the panhandle of Texas north into the Dakotas and east as far as Florida. They are unknown after the Hemphillian and are seldom found in late Hemphillian faunas. It should be emphasized that the map indicates limits of distribution and does not infer that these rodents occur or occurred everywhere within these limits.

It is a striking fact that neither of these families has been found in California later than the Eocene outside of the present distribution of Aplodontia. This complete absence is interesting in light of the occurrence of the earliest known aplodontid *Eohaplomys* in the Eocene of Southern California. These families in their post Arikareean development are not known south of the Great Basin. Their absence in California is based obviously on negative evidence. Such evidence must be carefully weighed especially when dealing with fossil faunas. The only faunas which were considered to present reliable negative evidence were those which included a representation of other rodents so that mylagaulids or aplodontids if present, might have appeared in the collections. It should be noted that although there are a number of localities in California which have produced rodents and other small mammals only a very few occur under conditions which

Fig. 22. Distribution of mylagaulid and aplodontid rodents in Western North America from Miocene to Recent. 1, McKay Reservoir, 2, John Day, 3, Paulina Creek, 4, Drewsey, 5, Juntura, 6, Skull Springs, 7, Sucker Creek, 8, Rome, 9, Beatty Butte, 10, Thousand Creek, 11, Virgin Valley, 12, Brady Pocket, 13, Smith's Valley, 14, Cedar Mountain-Stewart Springs, 15, Esmeralda-Fish Lake Valley, 16, Tonopah, 17, Cox Butte, 18, Abert Lake.

allows confidence in the completeness of a faunal list as concerns the small mammals. However, considering all these possible sources of error in the use of this negative evidence the author is impressed by the fact that in nearly a dozen of these localities there occur a number of small mammals, usually rabbits and often squirrels or beavers but no mylagaulids or aplodontids are known. It is on this basis that the absence of post Arikareean aplodontid and mylagaulid rodents in California is considered to be real and not an artifact of collecting.

The biogeographic history of these two divergent groups of rodents which stem from a common ancestor has long been noted by workers as unique. The aplodontids apparently arise and remain in Western North America whereas the mylagaulids appear all over temperate North America (except the extreme Southwest) almost immediately after their first appearance in the John Day Formation and maintain this distribution until their extinction in the Hemphillian. The aplodontids do not become extinct but reduce or shift their area into the Pacific slope of the Cascades and Sierras.

The Great Basin of Oregon, Idaho and Nevada is the crucial area in understanding the historical biogeography of these forms. The record here is limited to a sequence from Barstovian to Hemphillian. Since the fossil aplodontids of this sequence are not known outside this area (with the exception of the Asian record) and the development of the mylagaulids here is similar to that of the other parts of their range the discussion of related causal factors in their development and biogeography will be confined largely to the Great Basin.

It was mentioned above that the biogeographic histories of these two families are opposites. They are nearly as divergent in their morphologic changes. The mylagaulids reduce their dental formula from $\frac{1}{1}\ \frac{0}{0}\ \frac{2}{1}\ \frac{3}{3}$ in the Arikareean to $\frac{1}{1}\ \frac{0}{0}\ \frac{1}{1}\ \frac{0}{0}$ in adults of the Hemphillian (although small molars exist in young individuals). The animal as a whole greatly increases in size. The fourth premolar becomes much enlarged and its enamel pattern more complicated during its history. In contrast aplodontids retain the $\frac{1}{1}\ \frac{0}{0}\ \frac{2}{1}\ \frac{3}{3}$ dental formula to the present. They increase only moderately in size. The enamel pattern of the teeth does not become significantly more complicated. Neither group shows an increase in hypsodonty after the Barstovian. However aplodontids (in the *Liodontia-Aplodontia* line) develop ever-growing teeth. The premolar-molar series teeth of aplodontids retain their same relative size. Aplodontids have a living representative in *Aplodontia*. Mylagaulids have been extinct since the Hemphillian. Their only apparent points in common are their geographic and phylogenetic origins. They are both absent from the Great Basin after the Hemphillian.

The living *Aplodontia* is often referred to as a "living fossil." This conclusion is based on its "primitive" reproductive system and skeleton along with other anatomical characteristics studied by the comparative anatomists and embryologist. We have seen that there are only minor morphological changes since at least the Barstovian. *Aplodontia* at present is found almost exclusively in woodlands with rather steep slopes and abundant water. The slight changes in its morphology may indicate that its requirements were similar in the Barstovian. This line of reasoning usually of little value in the study of fossil mammals because of their rapid morphologic change may, however, lead to answers in the present problem.

Chaney and students have described a dramatic change in climate as demonstrated by vegetational change during the Tertiary in Eastern Oregon. This change consists of a transformation from a subtropical climate in the late Eocene to the semi-arid climate of today. This is accentuated by the rain shadow effect pro-

duced by the great height of the North-South Cascade Mountains attained in the Pliocene. Thus there is an increasing difference between the environments of western and eastern Oregon in the late Tertiary. As a result the present cover of western Oregon is more like that of Eastern Oregon of the Barstovian than that of today. This progressive change as related to the Great Basin is summarized by Axelrod (1950). The implication is that the aplodontids of the Barstovian could well have been in a similar habitat as that occupied by those of today. Their biogeographic history suggests that they either followed their habitat west or became restricted to the west thus not being greatly affected by the progressive climatic change.

Mylagaulids on the other hand, apparently became adapted to some grassland or grassland woodland-border situation. There is no direct evidence of this but their sudden much wider distribution in the later Miocene especially into the Great Plains correlated with the first appearance of extensive grasslands could be explained in this way. Their continued morphological change indicates an attempt to "keep up" with a changing environmental niche rather than to follow a particular one as did the aplodontids.

Figure 23 is a reproduction in part of Axelrod's (1950, fig. 4) summary of changing vegetational types. There is a correlation between the disappearance of mylagaulids and aplodontids in the Hemphillian (mid-Pliocene) with the extreme of climatic change resulting in the great reduction of woodland and coniferous forest in the Great Basin. This again suggests that the aplodontids were restricted into the Pacific slope area where they were able to maintain themselves until the present. This same change apparently removed or greatly altered the habitat of the mylagaulid too abruptly for them to compensate. The absence of forests in Mohavia throughout the later Tertiary and the minor woodland development in the Barstovian may account for the absence of these families to the South.

The points made above may be documented by a brief comparison of the changes in vegetation types and their distribution in the Tertiary of Western North America with that of the distribution of the rodents considered here. The maps of figure 24 will serve as a guide.

The maps show the area in which a particular plant element or Geoflora formed a dominant part of the vegetation. This does not mean that these elements or Geofloras as the case may be are not known outside the indicated areas or that other elements or Geofloras are not known within these areas of dominance. In the areas designated, the element or Geoflora involved made up the major portion of the vegetation. Local topographic features however undoubtedly allowed the development of islands of other vegetational types within the area of dominance of an element or Geoflora. (See Axelrod, 1956, fig. 16 for an example of this.) On each map the occurrences of each of the groups of rodents studied are indicated.

The vegetational history of western North America is described by the paleobotanist as a changing distribution of areas of dominance of three broad Geofloras. These Geofloras are named indicating their Tertiary origin, thus the Arcto-Tertiary Geoflora, the Madro-Tertiary Geoflora and the Neotropical Geoflora. The Arcto-Tertiary Geoflora has its origin to the north and contained conifers, broad leafed evergreens and deciduous plants, the morphological equivalents of which are found today in eastern Asia, western North America, and eastern North America. The Madro-Tertiary Geoflora which includes many of the plants of the present desert regions had its origin in the Sierra Madre. The Neotropical Geoflora contained subtropical plants many of which are found today in Central America and around the Caribbean. These Geofloras consist of ele-

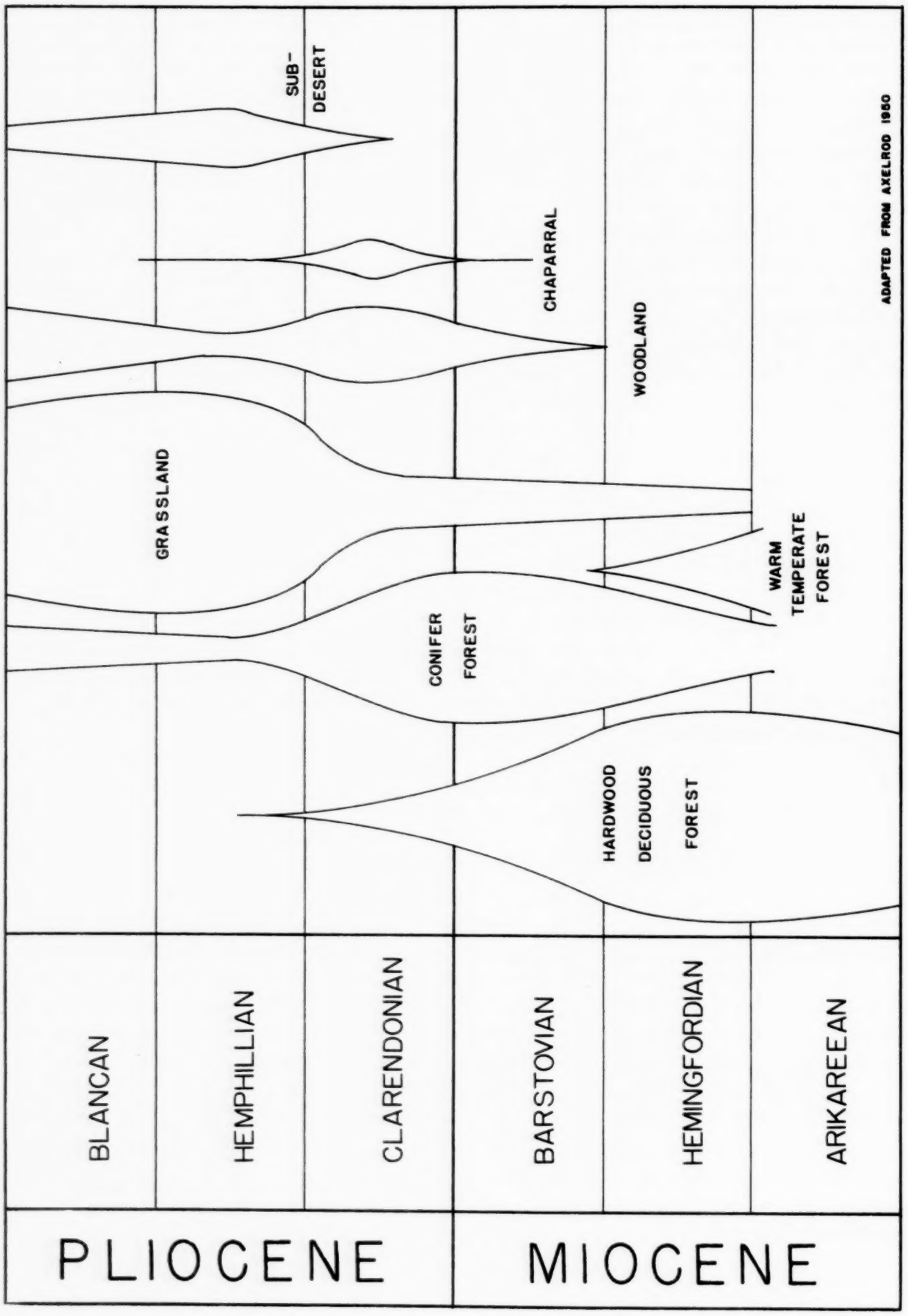

FIG. 23. Changing vegetation types in the Northern Great Basin.

ments which take their names from the present distribution of their living equivalent species. Thus the West American, East American and East Asian Elements of the Arcto-Tertiary Geoflora.

The Eocene and early Oligocene vegetation of western North America is dominated by the Neotropical Tertiary Geoflora. To the north and east the Arcto-Tertiary makes its appearance in the region of the Rockies. The earliest aplodont known, *Eohaplomys* from the Eocene Sespe Formation of southern California, is found within the limits of the Neotropical Flora. To the northeast *Pipestoneomys* a later aplodontid is known from the early Oligocene of Pipestone Springs, Montana (fig. 24).

By the later Oligocene the Arcto-Tertiary Geoflora occupied much of the Pacific Northwest. The early Miocene (Arikareean) John Day Formation of central Oregon has produced a number of Aplodontids. *Meniscomys,* usually classed with the aplodonts, occurs frequently in the middle John Day Formation. This early mylagaulid-aplodontid is known only from the John Day Formation. Soon after the appearance of this first "mylagaulid" the family extends its range to at least southern South Dakota. No members of the family appear to the south of the area occupied by the Arcto-Tertiary Geoflora. However, few records of fossil mammals of this age are known in Nevada and California, outside the later Sespe formation of Southern California (fig. 24).

Middle Miocene faunas are not known in the John Day Basin and are rare throughout the Pacific Coast. The record here is too poor to add to the present discussion. This period of time is crucial in aplodont-mylagaulid history for when these rodents are seen in the faunas of the Pacific coast of the later Miocene they have developed from the low crowned primitive rodents of the John Day to forms with high crowned teeth and many other advancements. They have, in fact, made their most important steps to the forms which typify them in all later species. The intermediate steps in the mylagaulid line can be seen in faunas from the great plains. It is as might be expected a rather quick development of higher crowned teeth progressing to the poorly rooted later Miocene species. No such intermediates are known from these plains faunas representing aplodontids as they never reached the area. They appear in the late Miocene faunas of Oregon and Nevada with high crowned teeth (as high as those living today) and with little to distinguish them from the living species. Vegetational changes within the Arcto-Tertiary Geoflora indicate a cooling and drying from John Day time to the late Miocene (Mascall).

The Arcto-Tertiary Geoflora consisted of three elements, West American, East American, and East Asian. Along the coast in more mesic conditions the East Asian and East American had largely replaced the Neotropical Geoflora and dominated the West American element by the late Miocene. The interior colder and dryer flora was dominated by the West American element. Aplodontids and mylagaulids are restricted to the West American element (fig. 24).

The Lower Pliocene and Middle Pliocene (Clarendonian and Hemphillian) distributions show essentially the same results, that is restriction of the two families of rodents to the area of West American element dominance and mylagaulids extending east into the dryer expression of the West American Element (fig. 24).

The recent distribution shows the only living representative, *Aplodontia* of the aplodontids to be restricted within the West American element area (fig. 24).

This apparent restriction of both families to the area of dominance of a particular vegetational group explains the lack of either family in the Southern California Tertiary after the appearance of *Eohaplomys* in the Eocene. If the map (fig. 24) is reviewed it shows that the

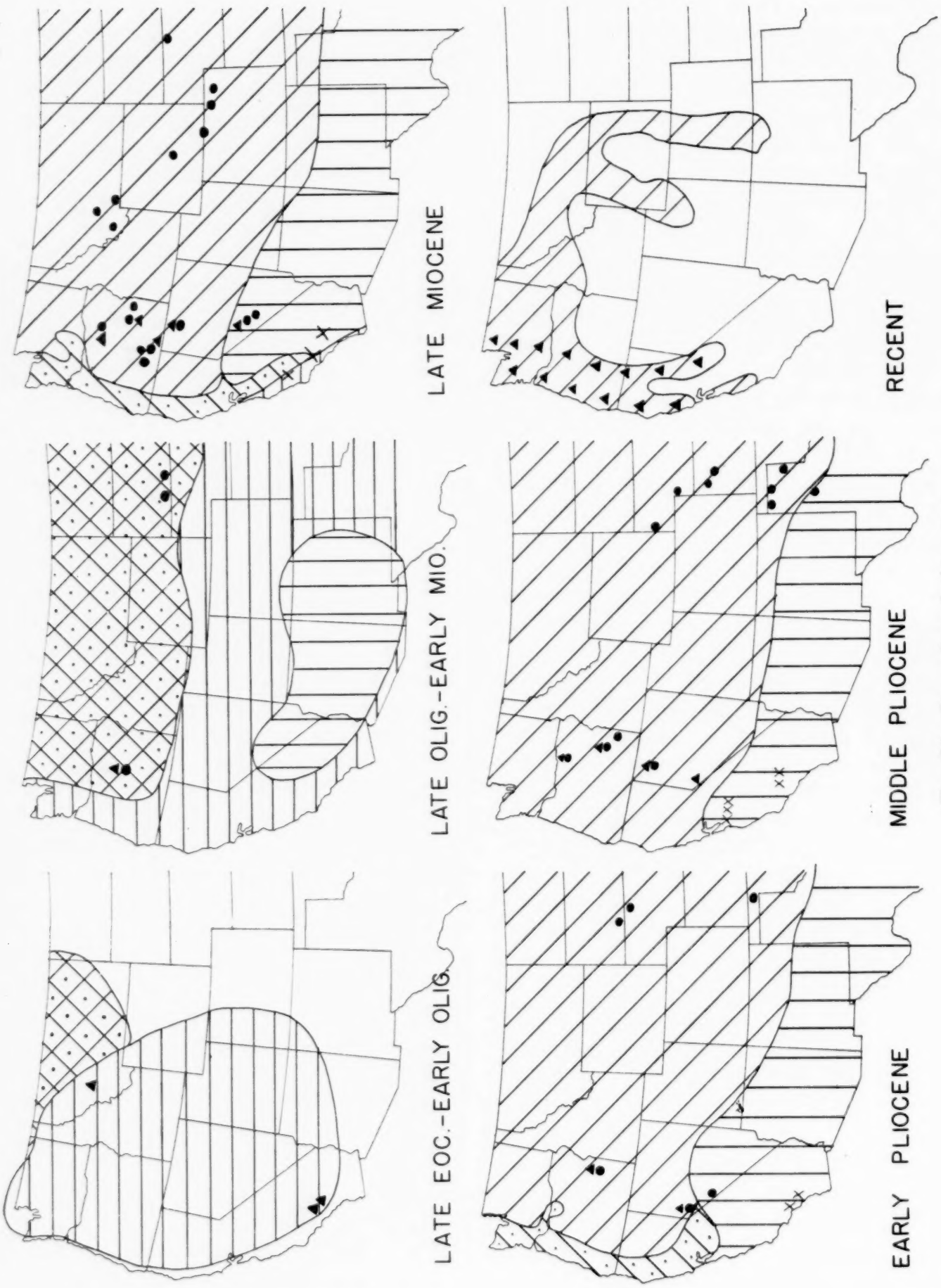

FIG. 24.—Legend on facing page.

explanation is something like this. The early Tertiary aplodontids were probably distributed throughout the Neotropical Tertiary forests of the Pacific Coast. With the diminishing of this vegetational type the aplodontids shifted to the mesic Arcto-Tertiary forests of the John Day and further to the less mesic West American element dominating the flora of that region in the late Miocene. This is also the time of the most morphologic change and diversity in Aplodontids. The aplodontids apparently stuck with the mesic forest component of the West American element, the mylagaulids with the dryer components. If this were the case then we would not expect to find any representatives of these families in Southern California after the late Oligocene since the West American element never dominated the flora there. We have few records of Tertiary fossil mammals in California north of the San Francisco Bay area and so cannot say that the families did or did not occupy that area which in part had a dominant West American element. Today *Aplodontia* occurs from the bay north coincident with the distribution of the moister West American Element.

It would appear then from this that these two families of rodents were tied rather strongly to particular vegetational formations after the Hemingfordian (middle Miocene). This was a vegetational type which happens to still occur near the apparent center of origin of the aplodontids.

Discussion

The history of the distributional changes of the family aplodontidae as seen above may be generalized as a reduction and possibly shift of range during the later Tertiary. Earlier Taylor (1918) indicated a similar history in his conclusion: "Apparently the range of the family Aplodontidae, as well as the genus *Aplodontia* [*Liodontia* was separated from *Aplodontia* later], was formerly much greater than at present . . . ." McGrew (1941) concluded in a study of the aplodontid distributional changes that "The range now occupied by *Aplodontia* is apparently near the center of origin and distribution of the family." From this early distribution the aplodontids expanded into the Great Basin and other areas only to return to their present and former distribution according to McGrew. He supports this view with the following:

1. "This is suggested by the occurrence of *Eohaplomys, Haplomys* and *Meniscomys* near or within the present range of *Aplodontia,* and at no other place." *Eohaplomys* is known only from Southern California just north of Los Angeles, several hundred miles south of the present range of *Aplodontia. Haplomys* and *Meniscomys* are known only in the John Day Basin of Eastern Oregon nearly two hundred miles east of the limit of the present distribution of *Aplodontia.*

2. "Occurrence of *Pseudaplodon* . . . and *Liodontia* suggests an early unsuccessful attempt to extend the range." This suggests an early unsuccessful ex-

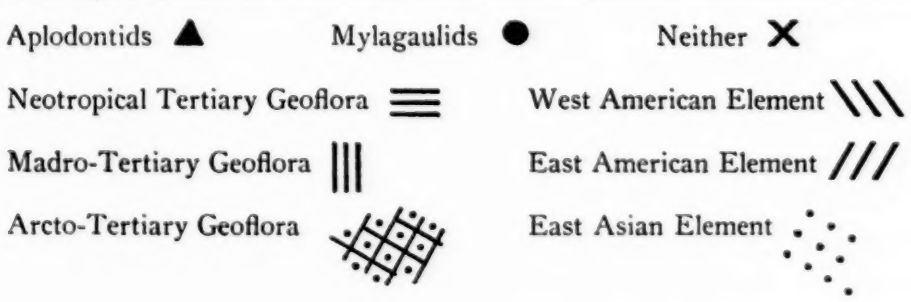

Fig. 24. Distributional changes in vegetation, and Aplodontid rodents in western North America.

tension of range only if the conclusion it is meant to support is true. In other words it represents circuitous reasoning adding nothing to the case.

3. ". . . these peripheral genera (*Pseudaplodon* and *Liodontia*) are somewhat more specialized than *Aplodontia*." Restudy of these genera shows this is not the case.

There is little reason to believe that the present distribution of *Aplodontia* is also the original distribution of the family. Even though the total area involved is somewhat limited when compared to other mammals it must be noted there is no direct evidence that aplodontids occupied their present range at all before the Pleistocene. This is not to say they did not, it is merely to remind us that we have few terrestrial Tertiary faunas from this area and none containing aplodontids. Hypotheses which infer this distribution are without basis other than the probable late occurrence here of aplodontids along with the West American floral element from the Mid-Pliocene on.

Apparently with Matthew's hypothesis in mind McGrew felt that "This distribution cannot be accounted for by any climatic or environmental change at the center of dispersal." However, the more probable distributional history of this group as presented in this study and earlier suggested by Taylor (1918) is explained through its close agreement with the changes in distribution of vegetation. One can conclude then that with the role of vegetation as a climatic indicator, climate must be considered an important factor in distributional changes of this family. This new understanding of the reaction of this family to climatic change as represented by vegetational change is not similar to what we believe is the case in many other groups of mammals. That is instead of changing markedly becoming extinct or migrating peripherally at the advent of climatic extremes the aplodontids change very little after the later Miocene, and move with their environment which is being sharply compressed to the west by the topographic changes in the Cascade Mountains and regional climatic change.

The study of this family of rodents affords us a unique opportunity to examine the relationship of plant and mammal distributional changes. I know of no other mammal whose distributional history can be so well defined and studied and correlated with evidences of floral change. The much greater distribution and diversity of most other mammals does not allow such a study. However, the present study can help in the explanation of the problems connected with the historical biogeography of these other families of mammals.

Acknowledgments

This paper is an outgrowth of work in mammalian community adjustment in geologic time. The American Philosophical Society first supported the original project which has been continued through support of the National Science Foundation. The author is not only indebted to these institutions but also to those who have loaned additional material for the study. They include University of California (UC), California Institute of Technology (CIT), and Yale Peabody Museum (YPM). The materials borrowed from the California Institute of Technology have since become the property of the Los Angeles County Museum. The illustrations of specimens were made by Mrs. Mildred Riechers Detling, the maps are by Robert Stevens and the diagrams by the author.

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THE ORIGIN OF SEXUAL ISOLATION BETWEEN DIFFERENT LINES WITHIN A SPECIES

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Introduction

If two or more species, sub-species or other taxa are to coexist for some length of time in the same territory, it is necessary both that each group should reproduce itself, and that the genetic systems of the different populations should not become intermingled. The mechanisms by which such a situation is ensured are usually spoken of as "isolating mechanisms." One form which they may take, and often do, is the development of mating preferences. It is worth noticing that if these are to operate successfully they must have certain characteristics. For instance, there may be mutations which cause an alteration in sexual behaviour, or in the structure of the copulatory organs, but these would not serve as a basis for an evolutionarily successful isolating mechanism unless they ensure a normal reproductive ability of the mutants. Moreover, when mating preferences occur, they must be complementary. If there are two strains A and B, it is not sufficient that A should mate with A more often than with B unless B also mates with B more often than with A, since otherwise strain B will soon get diluted out of existence.

We still know rather little about the origin of sexual isolating mechanisms. There are two main theories, usually associated with the names of Muller and Dobzhansky. Muller (1949) states that the impediments to gene exchange may arise by accident (chance), together with the processes of divergence of the genetic systems. They may be a by-product of other changes. There may be chromosomal genes, arisen by mutation, responsible for the incompatibility, but producing their isolating effect only in combination with other genes. Because of this fact, they "usually arise in populations separated from one another by outer circumstances. So, it is necessary to conclude, that isolating genes were not established by a process of selection which derived its original advantage from the achievement of the isolating effect itself, but were established, in their original local populations at any rate, through their selective value in other respects, or through drift, as the case may be."

Dobzhansky postulates an alternative or complementary hypothesis; physiological isolating mechanisms are a product of natural selection. "Development of all forms of reproductive isolation, including sexual isolation, between populations which have diverged sufficiently to make compromise genotypes unfavorable, may be initiated and furthered by natural selection" (Dobzhansky, 1941).

In Drosophila, certain strains show mating preferences which might provide a basis for the evolution of sexual isolation mechanisms. Thus Merrell (1949) found that certain mutant males (ct, y) mate more often with their own females than with wild type, but males from other strains also prefer these females. Thus these are a one-sided type of mating preference which cannot act as a satisfactory evolutionary isolating mechanism. A rather similar case has been described by Dobzhansky and Mayr (1944) who found that in the *D. willistoni* group females

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from Brazil are more readily inseminated by males from Guatemala and Brazil, the Guatemalan females being less receptive. More interesting is the finding (Dobzhansky, 1946, 1941) that, in the laboratory, there is greater isolation between populations of sibling species (*D. pseudoobscura-D. persimilis; D. pseudoobscura-D. miranda*) which have been collected from the same locality than between similar populations collected from different parts of the species range. This suggests that the isolation has been developed by the mechanism postulated by Dobzhansky, namely a selection for lack of crossing, occurring of course only in regions where crossing is a practical possibility. But although the facts are consonant with the hypothesis, we do not know exactly what has been going on in Nature, or whether this was in fact the way in which the isolation has arisen.

A few attempts have been made in the laboratory to develop isolating mechanisms between populations. Such experiments have the advantage, over the study of natural populations, that we know in some detail the nature of the evolutionary processes to which the populations have been subjected. They have the disadvantage that sexual vigour often tends to be considerably lower in laboratory strains than in the wild, which suggests that one should bear in mind the possibility that one may be dealing with somewhat atypical animals.

In laboratory experiments, Koopman (1950) was able to intensify the initially fairly low degree of mating preference between *D. persimilis* and *pseudoobscura* by selecting against the tendency to cross-breeding. Knight, Robertson and Waddington (1956), by a similar procedure, were able to bring into being, and considerably strengthen, a sexual isolation between flies carrying the mutants *vg* and *e*, which initially showed only a rather slight tendency to homogametic mating.

These two experiments tend to support the hypothesis of Dobzhansky. Knight, Robertson and Waddington also looked for evidence in support of Muller's suggestion, by examining the mating preferences of inbred strains which had been long isolated from one another, but which had never been subjected to any selection against cross-breeding. No such evidence was found, but only a very small number of lines were examined. In view of the great importance of sexual isolating mechanisms for the whole problem of the origin of species, it has been thought worthwhile to study the mating preferences of a number more strains of *D. melanogaster* which have originated in various ways and have been maintained separately for many generations. Any evidence of complementary mating preferences between such lines would give support to Muller's suggestion that such situations may arise by chance.

Stocks Used

We studied three types of lines, all of which had been maintained as separate stocks for a great number of generations by Clayton and Robertson in this laboratory.

1. *Selection lines.* Eight lines, all originated from Kaduna wild type, which had been selected for the number of chaetae on the 4th and 5th abdominal sternites. Four of them had been selected for a high number of chaetae:

H5/30/R36, selected for 30 generations, relaxed for 36 (H-5 in table 1)
H1/12/R15, selected for 12 generations, relaxed for 15 (H-1 in table 1)
H2/20/R46, selected for 20 generations, relaxed for 46 (H-2 in table 1)
H4/36/R35, selected for 36 generations, relaxed for 35 (H-4 in table 1)

Four had been selected for a low number of chaetae:

L1/29/R8, selected for 29 generations, relaxed for 8 (L-1 in table 1)

L2/29/R8, selected for 29 generations, relaxed for 8 (L-2 in table 1)
L4/20-1/R47, selected for 20 generations, relaxed for 47 (L-4 in table 1)
Li/31-3/R35, selected for 31 generations, relaxed for 35 (Li-1 in table 1)

2. *Inbred lines.* Six lines, also originally from Kaduna wild type, maintained by brother-sister matings for 57 generations. Three of them had been irradiated with X-rays previous to inbreeding: N20-1; N20-9; N20-2.

The other three had not been treated: NC-13; NC-4; NC-11.

3. *Isogenic lines.* Three stocks, originally isogenic, each with a different marker gene: *y* (yellow), *v* (vermilion), *w* (white). One line of each had been inbred, brother to sister for: *y*, 75 generations; *v*, 75 generations, and *w*, 76 generations; while three other lines had been maintained by simple mass cultures for: *y*, 64 generations; *v*, 67 generations, and *w*, 64.

Experimental Methods

In all cases we used the male choice method designed by Dobzhansky. For the selection and inbred lines, one male was placed in a vial with a female of its own kind and a female of another. The females were made recognizable by a spot of silver paint on the thorax of one of them. In the marked isogenic stocks, one to four males of one kind were placed in one vial with an equal number of females of its own and of another line.

Both males and females were collected within a few hours of hatching, aged in separate vials for 6 to 8 days, etherized and marked at least eight hours before testing. The matings with the selection and inbred lines were made in empty vials. The flies were observed for a period of 3 to 4 hours. The moment of initiation and the duration of the first copulation of the male were recorded. After 4 hours the females were dissected and examined for the presence of sperm in their ventral receptacles or spermathecae.

One line selected for a high number of chaetae was always tested with one with a low number of bristles: L-1 *v.* H-5; L-2 *v.* H-1; L-4 *v.* H-2; L[1]-1 *v.* H-4; and one of the irradiated lines was always tested to a non-treated line: NC-13 *v.* N20-9; NC-11 *v.* N20-1; NC-4 *v.* N20-2.

For the mutant stocks, males of one line were tested with females of both other lines, maintaining the inbred and the non-inbred as separate groups. The flies were left for 16 to 20 hours at 25° C, in vials with the usual Drosophila food medium. After this period the reproductive tract of all females was examined.

With the selection and the non-mutant inbred lines, a certain number of "female choice" tests were made. The combinations were the same as those mentioned above. One female was placed in an empty vial with a male of her own type, and one of the other line. (One of the males was marked with silver paint.) They were observed during three to four hours; the beginning and duration of the copulation was recorded. As during this time the female will only allow one copulation, the flies were discarded after the observation had been completed.

Results

Selection lines (table 1): On observation of the individual matings it could be seen that courtship began almost immediately after the introduction of the flies into the vial. Copulations started within the first two minutes, and most of them lasted for about 30 minutes. As can be seen from table 1, in most cases the first mating occurs more or less at random. The three significant deviations are not very large. In two of the L lines (L-1 and L-4) the males show a slight preference for the H female, while the H male shows random choice. This may indicate a higher receptivity of the H females, a fact also found by Knight, Robertson

and Waddington (1956). Only the L^1-1 male seems to prefer its own kind. During the four hours for which they have been together, the male may have copulated with another female (section 2). Now, in all except one case, the males have mated with an almost equal number of females of each type. Only the L-4 male maintains his significant preference for the H female. Analyzing the female choices (section 3), there seem to be a few more deviations from the random choice, but one can say that in general the same tendency as in the "male choice" is maintained. In any case, it seems that there are no consistent data in this group of tests suggesting that any type of preferential mating has become established.

TABLE 1. *Selection lines*

1. First Copulation

Male	Homo-gametic	Hetero-gametic	χ^2	Tend.	P.
L-1	12	23	3.4	−	sig.
H-5	25	21	.348	+	—
L-2	28	20	1.33	+	—
H-1	21	23	.091	−	—
L-4	14	26	3.8	−	sig.
H-2	26	19	1.089	+	—
L^1-1	14	6	3.2	+	sig.
H-4	12	17	2.79	−	—

2. Male Choice

Male	n	Homo-gametic	Hetero-gametic	χ^2	χ^2 (comb)	Tend.	P.
L-1(1)	25	10	17	4.349	2.174	−	−
L-1	25	14	14	0			
H-5(1)	25	21	13	5.882	1.277	+	−
H-5	25	16	19	.857			
L-2(1)	25	18	14	1.39	1.59	+	−
L-2	25	18	16	.37			
H-1(1)	25	16	13	.74	.199	−	−
H-1	25	14	19	2.23			
L-4(1)	25	9	17	4.701	6.429	−	sig.
L-4	25	9	14	2.013			
H-2(1)	25	18	16	.368	1.116	+	−
H-2	25	20	16	.787			
L^1-1(1)	25	5	5	0	1.114	+	−
L^1-1	25	11	6	2.228			
H-4(1)	25	9	7	.368	.399	+	−
H-4	25	10	9	.082			

(1) In the upper line of each group, the marked female was of the same strain as the male; in the lower line, the marked female was of the other strain.

−: tendency to heterogametic matings.

+: tendency to homogametic matings.

TABLE 1.—*Continued*

3. Female Choice

Female	n	Homo-gametic	Hetero-gametic	χ^2	χ^2 (comb)	Tend.	P.
L-1(2)	25	5	11	2.25	1.125	−	−
L-1	25	8	8	0			
H-5(2)	25	16	3	8.895	16.924	+	sig.
H-5	25	17	4	8.048			
L-2(2)	25	12	5	2.88	7.725	+	sig.
L-2	25	14	5	4.26			
H-1(2)	25	2	12	7.14	3.126	−	sig.
H-1	25	7	4	.82			
L-4(2)	25	8	12	.8	0.318	+	−
L-4	25	12	7	1.316			
H-2(2)	25	9	13	.727	0.845	−	−
H-2	25	9	10	.235			
L^1-1(2)	25	6	4	.4	0.2	+	−
L^1-1	25	4	4	0			
H-4(2)	25	13	1	10.286	3.468	+	sig.
H-4	25	5	7	.333			

(2) Marked male of same line as the female.

Inbred lines (table 2): The first fact in which these lines differ from the previous ones is in their generally diminished activity. The first copulation is initiated later, about 10 minutes after introducing the flies into the vial. It seems also that the total number of matings is less than in the non-inbred lines. There is a much greater correlation between the preference of the male for his first copulation (section 1) and the total number of homo- and heterogametic matings after four hours (section 2).

In the male choice experiments, in all three groups it seems clear that the non-irradiated inbred lines have a definite preference for their own kind, which may be attributable to a slightly greater activity of both unirradiated males and females. The irradiated males seem to mate more at random, although they seem to exhibit a slight tendency towards their own female. When females are allowed to choose between two types of males (section 3), mating is only slightly deviated from random. Only in NC-4 *v.* N20-2 is the preferential tendency significant for both the male and the female choice experiments. The NC females may be more attractive, both to their own and to other males. It is possible that in these inbred lines an incipient type of sexual isolation may have developed.

Isogenic lines (table 3): Both the inbred and the non-inbred lines behave in quite a similar way. After four to six hours very few copulations have taken place, so all matings were left for 16 to 20 hours at 25° C.

The most noticeable fact is the dislike all *non-yellow* females seem to have for *yellow* males, although yellow females accept all males with great intensity. This is a case of "one-sided preference."

Of the other two mutants, *vermilion* shows a slight preference for its own females, although this may be a consequence of a higher activity of both males and females.

White females seem to be the least re-

TABLE 2. *Inbred lines*

1. First Copulation

Male	Homo-gametic	Hetero-gametic	χ^2	Tend.	P.
NC–13	22	5	10.704	+	sig.
N20–9	8	8	0		–
NC–11	21	9	4.8	+	–
N20–1	16	9	1.9	+	–
NC–4	28	2	22.53	+	sig.
N20–2	2	12	7.14	–	sig.

2. Male Choice

Male	n	Homo-gametic	Hetero-gametic	χ^2	χ^2 (comb)	Tend.	P.
NC–13(1)	25	13	7	3	5.24	+	sig.
NC–13	25	13	5	3.62			
N20–9(1)	25	12	7	2.12	.660	+	–
N20–9	25	7	8	.09			
NC–11(1)	25	10	8	.43	4.406	+	sig.
NC–11	25	14	6	5.33			
N20–1(1)	25	11	9	.33	.166	+	–
N20–1	25	9	9	0			
NC–4(1)	38	24	11	9.133	27.44	+	sig.
NC–4	37	22	4	19.21			
N20–2(1)	38	5	8	.83	5.783	–	sig.
N20–2	37	4	13	6.18			

3. Female Choice

Female	n	Homo-gametic	Hetero-gametic	χ^2	χ^2 (comb)	Tend.	P.
NC–13(2)	25	5	1	2.6	2.06	+	–
NC–13	25	4	3	.14			
N20–9(2)	25	11	3	4	.27	+	–
N20–9	25	3	7	1.6			
NC–11(2)	25	5	14	4.26	.948	–	–
NC–11	25	11	8	.474			
N20–1(2)	25	6	2	2	.013	+	–
N20–1	25	5	7	.33			
NC–4(2)	25	8	6	.285	7.99	+	sig.
NC–4	25	12	0	12			
N20–2(2)	25	3	6	1	5.28	–	sig.
N20–2	25	0	5	5			

(1) Marked female of same type as the male.
(2) Marked males of same type as the female.
– : tendency to heterogametic matings.
+ : tendency to homogametic matings.

TABLE 3. *Isogenic lines*

(male choice)

Inbred

Male	n	Homo-gametic	Hetero-gametic	χ^2	Tend.	P.
y(F75)	100	58	4	68.163	+	sig.
v(F75)	100	93	76	11.032	+	sig.
y(F75)	100	47	0	47	+	sig.
w(F76)	100	33	37	.176	−	−
w(F76)	100	43	60	5.785	−	sig.
v(F75)	100	90	78	5.357	+	sig.

Not Inbred

Male	n	Homo-gametic	Hetero-gametic	χ^2	Tend.	P.
y(F64)	100	62	8	74.89	+	sig.
v(F67)	100	86	84	.157	+	−
y(F64)	100	74	3	106.4	+	sig.
w(F64)	100	65	79	4.861	−	sig.
w(F64)	100	23	51	16.873	−	sig.
v(F67)	100	90	57	32.44	+	sig.

+: tendency to homogametic matings.
−: tendency to heterogametic matings.

ceptive, even towards their own males, which shows a greater tendency towards heterogametic matings.

DISCUSSION

In these experiments we have found, with a few of the strains, rather definite evidence of a preference for homogametic matings. The evidence is strongest for the non-mutant inbreds examined. It is a remarkable fact that the three inbred strains which had not been X-rayed before inbreeding NC-13, NC-11 and NC-4, showed the greatest tendency of this kind, while in two of the radiated inbreds N20-9 and N20-1 it was rather feeble. However, in the other irradiated inbred N20-2 the mating preference was probably stronger than in NC-11, and it seems very unlikely that any particular significance should be attached to the radiation which had been administered to some of the lines many generations earlier, at least until many more similar comparisons are available.

Evidence of differential mating was also quite clear for the stocks marked with visible mutants. This is perhaps not very surprising, and the peculiar unattractiveness of yellow males was in fact known previously. A more puzzling, and perhaps more significant, fact is the observation that a tendency towards sexual isolation is much less noticeable among the selected lines than it is among the inbreds. Two factors may contribute to this. In the first place, if, following Muller, we suppose that the mating preferences arise by the chance alteration of the gene pools of the two populations, they will be the more likely to arise the wider the spectrum of genes which are affected. When a stock is selected in two directions, the resulting strains may be expected to differ primarily in those genes which affect the character on which

selection was exercised, whereas when a series of inbred lines are prepared from one foundation-stock the genotypic differences which arise by chance should not be confined to any particular category of phenotypic effects. Secondly, during the preparation of a series of inbred lines by setting up pair matings, only those families will survive in which the mating habits of the parents were at least compatible; and this may in effect amount to a certain degree of selection favouring homogametic mating.

In nature, the evolution of sub-specific strains adapted to different environments would probably, in these two respects, resemble the development of inbreds rather than the selected strains of the laboratory. It is likely to be very rare for natural selection to operate on any single phenotypic character of a restricted kind comparable to the "number of abdominal chaetae" for which selection was made in the stocks tested here; and again in the formation of subpopulations there will be some intra-population selection for sexual compatibility. Thus the fact that tendencies for inter-population isolation have been found in the inbreds, where they must have arisen by chance, seems rather good evidence that the processes suggested by Muller may actually occur in Nature. The major element of doubt in the situation arises from the reduction in general sexual activity which characterizes the inbreds.

The discrimination found was much more marked when males have a choice of two females, than when a female can choose between two males. Merrell (1949a) states the female choice is more indicative of discriminative behaviour, but, in both types of experiments, it may very well be that it is the female which exercises the discrimination, by either accepting or rejecting the male. The "male choice" experiment may indicate the greater or lesser receptivity of the female to a particular male, while the "female choice" method may be indicative of competition between males. More direct observation of behaviour is necessary before one can state in which way the male and the female of two lines may react to one another.

In the lines with mutant markers, the female seems to be the one responsible for a higher or lower discrimination. Several authors have studied the yellow mutation: in *D. subobscura* (Rendel, 1944), and in *D. melanogaster* (Merrell, 1949; Bastock, 1956), and they have agreed on the lesser receptivity of non-yellow females for yellow males. In *melanogaster* (Bastock, 1956) an important factor seems to be a less stimulating effect of the yellow male; the higher receptivity of the yellow female to both its own and to other males may be an indication of an adaptation of this female to the altered behaviour of the male. In the case of white, the female seems to be less acceptable to any male.

What may be the cause for these mating preferences? It has been postulated that smell may play an important role (certain moths, spiders, cf. Dobzhansky, 1941), although in *D. pseudoobscura* and *D. persimilis* Mayr and Dobzhansky (1945) find that the intensity of sexual isolation is not modified if larvae of both species are grown on the same food. Cutting off antennae also does not seem to alter the response significantly, although it does diminish discrimination of females for winged and wingless males (Bastock, 1956).

Summary

1. A search was made for the existence of mating preferences between strains of *Drosophila melanogaster* which had been genetically isolated from one another for many generations, but in which no selection or other procedure which would be expected to influence inter-strain mating had been practiced. The mating preferences were investigated by (i) allowing males to choose between females of their own and another strain, and (ii) allowing females a similar choice between males.

2. The strains studied were: 8 "selected lines," 4 of which had been selected for high numbers of abdominal chaetae and 4 for low numbers; 6 inbred lines of wild type phenotype; 3 isogenic stocks carrying the marker genes yellow, vermilion and white.

3. The marked isogenic stocks differed from one another in general sexual vigour, and all non-yellow females show an aversion to yellow males; yellow females are very receptive towards males of any kind.

4. In four out of the six inbred lines there was a statistically significant tendency in the male choice experiments for matings to be homogametic, and in two of these four the same tendency was found in the female choice experiments.

5. Among the selected lines mating seemed to be nearly at random.

6. It is argued that the fact that tendencies to homogametic mating may arise by chance within inbred lines provides rather good support for the suggestion that the initial steps towards sexual isolation between populations in nature may also be sometimes attributable to chance.

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STUDIES ON HETEROZYGOSITY AND HOMEOSTASIS II: LOSS OF HETEROSIS IN A CONSTANT ENVIRONMENT[1]

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INTRODUCTION

The widespread occurrence of genetic polymorphism in natural populations of plants and animals is one of the most puzzling facts of evolutionary dynamics. Some part of the observed genetic variability in nature is due to recurrent mutation and such variability poses no serious problem of understanding. On the other hand, a great deal of natural variability within a population, perhaps the most significant part, seems to be maintained by the mechanism of heterosis. In nature, heterozygous genotypes often have a higher fitness or adaptive value than the homozygotes produced by recombination from them, and it is this greater fitness of heterozygotes which is responsible for the continued genetic heterogeneity of the population. The problem that arises is to explain the widespread occurrence of heterotic or balanced polymorphic systems. One must either argue that heterozygosity *per se* confers greater fitness on an organism because of some biochemical mechanism basic to all living matter, or else that the higher adaptive value of heterozygotes is itself a product of evolution. In favor of the former view one might propose a mechanism like that suggested by Sewall Wright (1934) for the phenomenon of dominance. Wright pointed out that the very nature of the kinetics of enzymatic reactions will produce dominance of genes that produce more of a substance (hypermorphs) over those that produce less, or none at all (hypermorphs or amorphs). Fisher on the other hand (1928) considered dominance to be a product of natural selection, not a basic biochemical fact of life. While the origin of dominance is no longer a burning issue in evolutionary theory (although indeed the problem is no better settled than it was 25 years ago), the origin of heterosis is a real and important issue.

No student of evolution, as far as I know, is prepared to argue that heterosis is an ineluctable biological law. Rather, there seems to be universal agreement that balanced polymorphism has arisen in the course of time as *one of a number of* evolutionary modes. The most succinct statement of this view is Mather's (1955) that "Genetical principles do not rest on physiological arguments." Lerner, in his book, "Genetic Homeostasis" (1954), argues strongly and convincingly for a special value of heterozygosis, yet he carefully points out that this is a property of sexually reproducing populations. No claim for greater fitness of heterozygotes is made in the case of self-fertilizing species, for such organisms have clearly foregone the advantages of heterozygosity in the course of realizing their particular evolutionary mode.

THE ORIGIN OF A HETEROTIC SYSTEM

How does a balanced polymorphic system arise in a population? First it might be supposed that mutations occur which, fortuitously, are more fit in heterozygous condition than the homozygotes already in the population. Simply by intra-populational selection the frequency of these

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mutant alleles would increase to an equilibrium point and thereafter be maintained. If balanced polymorphism is to be a common pattern this process must be frequent and the occurrence of a random heterotic mutation cannot be a rare event. Such a process, however, contradicts the assumption in the previous section that random mutations are not heterotic *per se* but only in populations which already have heterosis as part of their historically determined pattern. On the other hand, if a population in which heterozygosity is already the rule, is made artificially homozygous through rapid inbreeding, then random mutations *will* be expected to show some heterosis. This is in fact what Wallace (1957) has shown to be the case.

If intra-populational selection is not responsible for the origin of heterotic systems, there must be some selective advantage conferred on a population as a whole by polymorphism. Should polymorphic systems tend to survive longer than monomorphic ones, there would be a gradual replacement of monomorphic by polymorphic systems. It is reasonable to suppose that a genetically polymorphic system will tend to survive longer because of the flexibility conferred by polymorphism in the face of variable environment. A population with a single genotype will be able to live and reproduce in a relatively restricted range of environments. Taking temperature as an example, a given genotype may be viable and fertile between 15° C and 25° C. A second genotype may have no wider range of temperature tolerance, but it may extend from 12° C to 22° C. A population which contains both these genotypes will then contain some members capable of surviving over the range 12° C to 25° C as compared with the smaller range of a monomorphic group. Since environment in nature is forever fluctuating within broad limits, only those populations with broad tolerance ranges will survive for protracted periods. There are, of course, exceptions as in the case of certain endoparasites and marine organisms whose survival over geologic time is a result of the unusual constancy of their environment. It is a commonplace of plant ecology that the range of a species is adjusted not to average temperature, rainfall, etc., but is limited by the extremes of these factors. What is true in space is certainly true also in time.

Thus the rise of polymorphic systems as an evolutionary mode is dependent upon the greater survival ability of polymorphic populations in an ever-changing environment. The only alternative to this conclusion is that heterozygosis *per se*, independent of the evolutionary history of the species, has a basic biological superiority.

The Maintenance of Polymorphism

In a balanced polymorphism population homozygotes may arise that are more fit than heterozygotes in a given environment. An example of this can be found in the experiments of Dobzhansky, Pavlovsky, Spassky and Spassky (1955). They measured the larval viability of 178 strains of *Drosophila pseudoobscura*, each strain homozygous for the second chromosome. About 10% of these strains had viability equal or superior to the average of heterozygotes, although none was as viable as the best heterozygote. Nevertheless, under the experimental conditions of temperature and food, some homozygous genotypes were definitely more fit than the vast majority of heterozygotes. If there are homozygotes which are so highly fit, why is it that the population from which these animals were sampled remains so highly polymorphic? The answer is found in the second part of the experiment just described. When the homozygotes which had high viability at 25° C and with Fleischman's yeast as a food source, were tested at other temperatures and with other species of yeast, not one of them maintained its high viability. The heterozygotes on the other hand showed uniformly high viability in

all of the nine environments tested. Thus, on the average over all environments, no homozygote was found which was as viable or more viable than the average of heterozygotes. In Dobzhansky's terms the homozygotes are "narrow specialists" which, although capable of superior performance in a narrow range of environments, are not well adapted to a great range of conditions. In contrast the heterozygotes while inferior to a few specialized homozygotes in specific environments, evince a higher overall fitness.

It is thus the variation in environment which is instrumental in the maintenance of polymorphism, as it is on the origin of a balanced system. The greater populational homeostasis of a polymorphic system has given rise to polymorphism as an evolutionary mode. The greater individual homeostasis of heterozygotes in sexually reproducing populations is the chief mechanism by which this polymorphism is maintained.

The Loss of Polymorphism

If it is correct that variation in environment is responsible for the origin and maintenance of balanced polymorphism, it ought to be possible to destroy a polymorphic system in the laboratory by maintaining a population under as nearly constant conditions as possible.

In order to see the destruction of a polymorphic system within a reasonable time, an already established balanced polymorphism with the following characteristics is needed:

a) Simple inheritance. Preferably the phenotype should be determined by a single Mendelian factor.

b) Sufficient genetic variability at the locus in question. Since the loss of the polymorphism will depend upon the occurrence of an allele or alleles which are more fit in homozygous condition than in heterozygous condition, and since these are in the minority in any given environment, variability must rapidly be made available.

These conditions are admirably fulfilled by the naturally occurring inversion systems in *Drosophila pseudoobscura*. Most populations of *D. pseudoobscura* are polymorphic for structural rearrangements on the third chromosome. Because the rearrangement suppresses crossing over between homologous chromosomes in the heterozygote, each karyotype acts in inheritance as a single Mendelian factor. However, no two chromosomes with the same arrangement carry the same gene alleles and recombination is perfectly free between two homologous chromosomes with the same inversion configuration. Thus within the gene pools of a given structural arrangement there is an immense genetic variability. There is, in addition the occasional double cross-over in inversion heterozygotes, which will further enhance the variability.

In certain populations the different inversions are maintained in a balanced polymorphism which shows cyclic changes. (See Dobzhansky, 1951, and Epling, Mitchell and Mattoni, 1957, for a general review of this work.) At some times of the year one inversion type will increase in frequency at the expense of others, while at other times it will decrease. This change repeats cyclically with the cyclical alteration in seasons, and is apparently due to changes in the relative fitness of the inversion homozygotes. The problem of the relative fitness of inversion heterozygotes is somewhat complicated due to conflicting experimental results. Dobzhansky and Levene (1948) found heterozygotes to be significantly more frequent than expected on the basis of Hardy proportions, but Epling, Mitchell and Mattoni found no such excess and indeed found a deficiency of heterozygotes in some cases.

The general picture which emerges is that of a polymorphic system maintained by fluctuation in fitness of structural homozygotes and superior fitness of at least some heterozygous types. In laboratory populations Wright and Dobzhansky (1946) have shown clearly that stable

polymorphic systems can be formed by these inversion types and that the heterozygote between two inversion types has a distinctly greater fitness than either of the homozygous types. Thus, if a population is begun with equal frequencies of two inversions, say Standard and Chiricahua, an equilibrium will be reached in which Standard is at a level of about 70% and Chiricahua 30%. Mathematical analysis then shows that the adaptive values or fitness of the three genotypes are in the order

Heterozygote > Standard homozygote > Chiricahua homozygote.

That is, the polymorphism is maintained by heterosis.

None of these cages has been kept for much more than 400 days or about 16 generations, however. It seemed reasonable that if such a population were maintained for a much longer period with as constant conditions of temperature and food supply as it is possible to maintain, homozygotes might arise which were superior in fitness to the heterozygotes, with a resultant loss of the heterotic system. The following experiment was performed to test this hypothesis.

Experimental Procedure

The experimental populations used were originally set up by Prof. Dobzhansky for another purpose and I am greatly obliged to him for allowing me to sample these populations for my own experiments. Dobzhansky's two initial populations, A and B were each started with 50% Pikes Peak and 50% Arrowhead gene arrangements derived from a population of *D. pseudoobscura* at Austin, Texas. Each population was made by crossing 12 different strains of Pikes Peak homozygotes with 6 different strains of Arrowhead homozygotes. Since each strain was descended from a single structurally homozygous wild female inseminated by a homozygous male, there were 48 different Pikes Peak and 24 different Arrowhead chromosomes represented. These cages and all others which will be discussed were maintained in constant temperature cabinets at 25° C using the population cage technique described by Wright and Dobzhansky (1946). After 200 days half of the food cups from population A and half from population B were removed and placed in a single new cage, C, which was then taken to Raleigh from Prof. Dobzhansky's laboratory for the rest of the experiment. Cages A and B were discontinued after 365 days while population C was continued. After 510 days a new population, D, was broken out of C as a replicate. This replicate population was continued until the 770th day of the experiment when it was lost due to contamination with *D. melanogaster*. At 900 days, a new population, E, was broken out of C as a replicate and these two cages were continued until 1130 days of the experiment had elapsed, a total period of approximately 44 generations. There is no exact information on generation time in population cages and as a matter of fact the generations are completely overlapping after a short time, but at 25° C the average time from egg to egg is estimated by Dobzhansky and Levene (1951) as 25 days.

Samples of eggs were collected from the cages at intervals and the larvae hatching from these eggs were dissected for salivary gland slides in order to determine their chromosomal configuration. Each sample was of 150 larvae or 300 chromosomes.

Experimental Results

The results of the chromosome determinations are shown in table 1 and figure 1. What is presented in both the table and figure is the frequency of Arrowhead chromosomes in each sample for each cage.

There was a rapid rise in the frequency of AR chromosomes for the first 200 days followed by a distinct leveling off until the 550th day. Cages A and B followed each other quite closely until the time

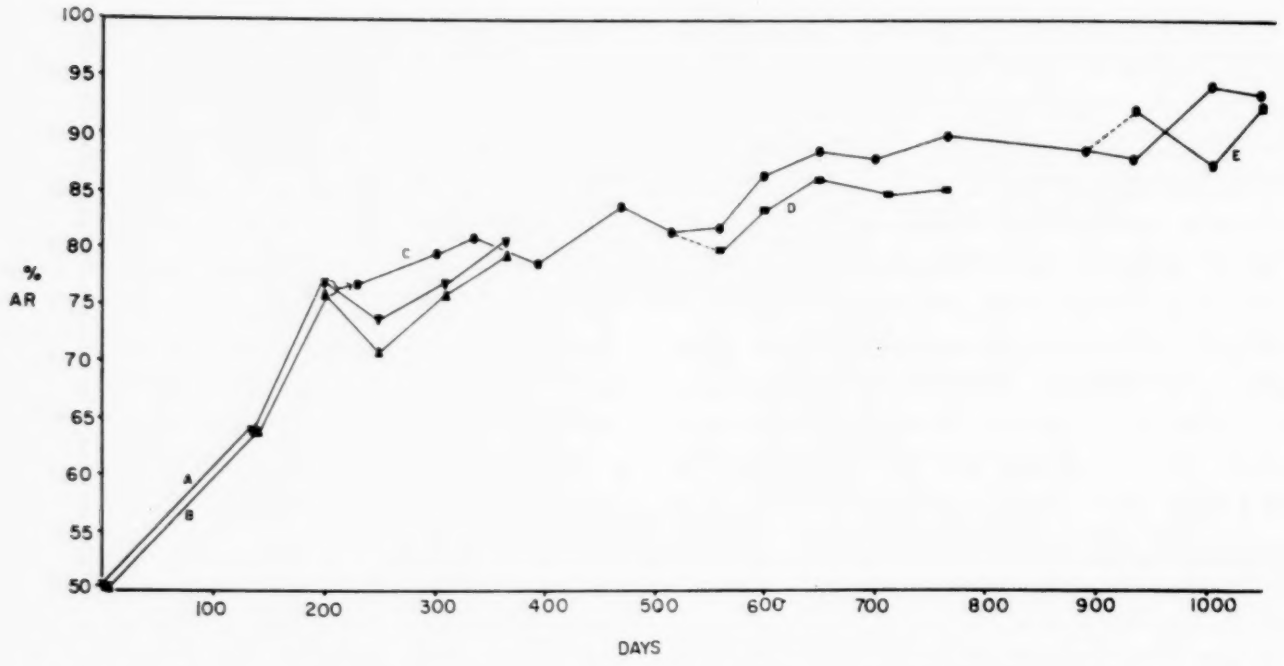

FIG. 1. Per cent Arrowhead chromosomes in populations A, B, C, D and E at various times. Ordinate in per cent Arrowhead. Abscissa in days. (▼−▼) A; (▲−▲) B; (●−●) C; (▬−▬) D; (⊗−⊗) E.

that they were terminated. Cage C, even though maintained in a different laboratory, was in quite good agreement with these two during the period when they were contemporaneous. Apparently populations A, B and C were coming to an equilibrium at about 83% to 85% Arrowhead. After the 550th day, however, a new rapid rise occurred in cage C and D and continued until the cages were terminated at 1130 days. The final frequency was in the neighborhood of 93% in both cages C and E. This rise was steady from the 600th day of the experiment (about 24 generations) and there was no sign of equilibrium after that time. The rate of fixation of the common gene arrangement AR is bound to be slower and somewhat erratic after it has reached 95% since selection is extremely inefficient in eliminating a rare allele. For this reason it was not felt that any purpose would be served in continuing the experiment longer than 1130 days.

TABLE 1. *Per cent AR chromosomes observed in populations A, B, C, D and E at various times*

Days	Populations				
	A	B	C	D	E
0	50.0	50.0	—	—	—
140	64.0	64.0	—	—	—
200	76.0	77.3	—	—	—
230	—	—	77.0	—	—
250	71.0	73.7	—	—	—
290	—	—	79.7	—	—
300	75.7	77.0	—	—	—
335	—	—	81.0	—	—
365	79.3	80.3	—	—	—
395	—	—	78.8	—	—
470	—	—	83.7	—	—
515	—	—	81.7	—	—
560	—	—	82.0	80.3	—
605	—	—	86.3	83.7	—
650	—	—	88.3	86.6	—
695	—	—	87.7	—	—
710	—	—	—	85.0	—
770	—	—	90.0	85.7	—
890	—	—	88.7	—	—
930	—	—	87.7	—	92.0
1010	—	—	94.3	—	87.3
1050	—	—	93.3	—	92.7
1130	—	—	94.7	—	91.6

Several attempts were made to fit conventional selection coefficients to these results by the method of Wright and Dobzhansky (1946) and Dobzhansky and Levene (1951). These curve fitting procedures met with no success because the selection coefficients of the three genotypes were changing throughout the

course of the experiment. No model which includes constant selection coefficients can explain the steady, almost linear, rise of the frequency of AR after 600 days. This rise can only be explained by a gradual change in the fitness of AR homozygotes in relation to PP homozygotes and PP/AR heterozygotes.

If the various replicate values are averaged, the rise in AR frequency in the first 8 generations was 3.31% while in the next 14 generations only 0.32%. This is a reflection of the equilibration of gene frequencies which is usually observed in a balanced polymorphic system with superior heterozygotes. During the last 22 generations, however, the gene frequency rose at a rate of 0.55% per generation which is not in accord with the behavior of a balanced heterotic population.

There are two possible explanations for the continued rise in the frequency of AR. First, it is possible that the adaptive values of the three genotypes are functions of the frequencies of these genotypes themselves. This has been observed for inversion by Dobzhansky, Pavlovsky and Levene (1954) and Spiess (1957). The second, and more interesting, possibility is the one suggested at the outset: that recombination and natural selection have changed the genetic content of the Arrowhead and Pikes Peak gene arrangements in the population in such a way as to favor structural homozygotes.

To distinguish between these alternatives a second experiment was performed. At 650 days population C was sampled and adult flies allowed to hatch from the sample. Males and females were mated in single pairs and larvae from each of these matings were scored. In this way strains homozygous for Arrowhead and for Pikes Peak were derived from the population. Because of the low frequency of Pikes Peak in the cage it was necessary to go through 3 successive generations of single pair matings from the original samples to secure homozygous strains of PP. The result was 6 strains of PP comprising 12 different PP chromosomes and 10 strains of AR comprising 40 different AR chromosomes.

TABLE 2. *Makeup of cages constituted from original (OR) and rederived (RE) chromosomes*

Cages	AR	PP
F	OR	OR
G	OR	RE
H	RE	OR
J	RE	RE

In addition to these rederived chromosomes the original strains of PP and AR from which the cages had been started, had been maintained in the laboratory as separate strains in bottles at 19° C. Considerable past experience in Prof. Dobzhansky's laboratory has shown that maintenance of inversion stocks in this way does not materially affect the results of population cage experiments. Populations started with strains recently derived from the wild show the same changes in inversion frequency as do those begun from strains maintained in the laboratory for many generations.

From the rederived chromosomes and the original chromosomes four new populations were started each with 50% AR and 50% PP. The make-up of the four cages as shown in table 2 and in table 3 are the results of a sample taken from each of these cages after 60 days.

Cage F is simply a replicate of the original populations while cages G, H and J contain one or both inversion types rederived from population C.

TABLE 3. *Frequency of AR inversion in cages F, G, H and J when initiated and after 60 days*

Cage	% AR 0 days	% AR 60 days
F	50	52.7
G	50	58.7
H	50	70.7
J	50	71.3

TABLE 4. *χ^2 tests for differences among populations F, G, H and J at 60 days*

Comparison	χ^2	P
F–G	2.18	.10–.20
H–J	0.03	.90–.95
F–H	20.56	<.001
G–H	9.46	.01–.001
F–J	22.18	<.001
G–J	10.58	.001

The result of this second experiment, as shown in table 3, is quite clear. Cages F and G which contain the original AR chromosomes show a small increase in the frequency of AR which compares closely with the rate of change in Dobzhansky's original cages A and B during the same period. By reference to figure 1 it can be seen that at 60 days AR must have been in the neighborhood of 55 to 56%.

Cages H and J, however, which contain reselected Arrowhead chromosomes rose sharply in these first two generations. Table 4 containing the result of χ^2 tests for the difference among the populations shows that F and G are not different from each other nor are H and J but there is a highly significant difference between the F-G and H-J groups.

DISCUSSION

It was pointed out that the failure of the original populations to establish a long-lived equilibrium and the apparent change in the adaptive values of AR homozygotes, PP homozygotes and AR/PP heterozygotes during the course of the experiment might have two explanations. If the first explanation were correct, that the adaptive values of these three genotypes are functions of the frequencies of the arrangements in the population, then rederived PP and AR chromosomes ought to show about the same adaptive properties as the original chromosomes. This would mean that cages F, G, H and J should all have behaved similarly and in a manner similar to the original populations. This is not the case. The two populations G and H that contained rederived AR chromosomes showed a much more rapid rise in gene frequency than did those containing original AR strands. This can only be due to a change in the average gene contents of AR chromosomes between the initiation of cages A and B and the time of the rederivation of chromosomes 600 days later. Moreover, this change was in the direction of an increase in the fitness of AR chromosomes when homozygous. The gradual increase in the frequency of AR in the original cages shows only that AR homozygotes are increasing in fitness relative to heterozygotes and PP homozygotes in the population. The results of the rederivation experiment show more than this. They demonstrate that PP homozygotes did not suffer any demonstrable loss of fitness and in fact if the comparison of cages F and G are taken at face value it must be assumed that this was a slight decrease in the adaptive value of this genotype. More important, the AR chromosomes increased in fitness not merely relative to PP homozygotes but relative to the original unselected AR strains.

A further confirmation of the notion that the gene contents of AR chromosomes changed during the course of natural selection in the cages, is found in the behavior of replicate populations. The original three populations, A, B and C, behaved in a very similar manner. There was an unaccountable drop in the frequency of AR in cages A and B just after cage C was broken out from them. This may have been due to the sampling itself or to some unknown change in the environment. The cages recovered rapidly, however, and when they were terminated they contained the same percentage of AR as did replicate C. This similarity of behavior in the three replicate populations at the start of the experiment is indicative of the strong natural selection acting upon the structural ho-

mozygotes and heterozygotes as single entities which were much alike in the three populations. In contrast to this is the behavior of populations C and D from 510 days until the loss of cage D. While these two replicates showed the same sorts of fluctuation and general trend, they slowly diverged during the 10 generations of the life of population D. This slow divergence of the two populations is indication of changes occurring *within* the AR and PP gene pools, changes which took place at different rates in the two populations. Had the change in fitness of the genotypes been entirely due to change in frequency of the inversions in the population, the two replicates would have behaved identically. It was only because selection was altering the genetic contents of the chromosomal types that this difference is observed.

The course of events in population C and its replicates can be reconstructed something as follows:

In nature a balanced polymorphism existed in which PP/AR heterozygotes had a higher adaptive value on the average than did either PP or AR homozygotes. It is likely that in a fluctuating environment one homozygote is sometimes more fit and sometimes less than the other. This change of fitness coupled with the greater fitness of heterozygotes on the average maintains the natural polymorphism. When the inversions were brought into the laboratory and set up in an artificial population with relatively constant environment, the direction of selection changed drastically and new combinations of genes were favored. Nevertheless, the superior homeostatic properties of the structural heterozygotes allowed a new stable polymorphism to be set up in the early stages of the population. This was the situation up to about 20 generations. During these 20 generations and thereafter, however, recombination within AR and PP gene pools had been taking place and some of these combinations were particularly fit in the fairly stable laboratory environment. Gene frequencies within the two gene pools were changing in response to the unidirectional natural selection but considerably more rapidly in the AR gene pool than in the PP. This is because PP homozygotes were relatively rare for most of the life of the population. At a frequency of the AR arrangement of 80%, 64% of the flies in the population were homozygous AR, 32% were heterozygotes while only 4% were homozygous PP. As a result, recombination and selection among PP chromosomes was not very efficient. This accounts for the failure to observe any significant change in the rederived PP strands in the second experiment. The gene contents of the PP pool were selected almost entirely on the basis of the fitness of structural heterozygotes, while the genes in the AR pool were subject to selection in structural homozygotes and heterozygotes, but mostly the homozygotes. The end result of this selection process was the establishment of structural homozygotes which were as fit or more fit than heterozygotes, thus causing the destruction of the balanced polymorphism.

It should not be supposed that heterozygosity for the inversion in question and genic heterozygosity at the level of the recombining locus are the same thing. There is no evidence that the AR gene pool which resulted from selection is any more homozygous at its various loci or even that the total amount of genic heterozygosity has changed in the populations. It is only the gross structural polymorphism which has been upset. If the theory presented here is correct then the total genic homozygosity should also have increased but there is absolutely no evidence on this point.

It might be argued that the loss of the polymorphism was entirely due to the high frequency of AR homozygotes at the initial equilibrium, the question of constancy of environment being irrele-

vant. I have pointed out that the rarity of PP homozygotes certainly influenced the course of the selection and made possible the rapid improvement of the AR gene pool. However, the critical factor remains the fairly constant direction of natural selection. That this is true can be seen from the data on the proportions of these inversion types in nature. In the region of Texas from which flies for this experiment were obtained the rough figures for the frequencies of different gene arrangements are 21% AR, 70% PP, 9% miscellaneous rare arrangements. (Data from Dobzhansky, 1944.) These values give the following figures for genotypes: 49% PP homozygotes, 29% PP/AR heterozygotes, 4% AR homozygotes and 18% assorted rarer homozygotes and heterozygotes. In nature, then, one homozygous type is quite rare, while the other represents the most frequent genotype, a situation exactly parallel to that in the laboratory population although the particular arrangements are reversed in their frequency. The polymorphism in nature is a persistent one, despite a preponderance of PP homozygotes. This, presumably, is because no single structural type is as uniformly favored in nature as it is in the laboratory population. It would be desirable to demonstrate in a laboratory population that fluctuating environment will maintain the polymorphic system. Unfortunately no one has yet found the kind of environmental change that will reverse the relative adaptive values of inversion homozygotes. It is this sort of fluctuation, mimicking the natural situation, that would be necessary for such an experiment.

Summary

The rise of balanced polymorphism as an evolutionary mode in sexually reproducing organisms has been a result of inter-populational selection. Polymorphism is a homeostatic device by which populations can persist despite fluctuation in environment. The maintenance of balanced polymorphism in a population is also contingent upon environmental variability. This hypothesis was confirmed by the following experiment. A population of *Drosophila pseudoobscura* containing two third chromosome inversions, Arrowhead and Pikes Peak, was established under quite constant conditions of food, moisture and temperature. The frequencies of the inversion reached an equilibrium state at about 83% Arrowhead and remained in that balanced condition for several generations. Thereafter a sudden increase in the frequency of the Arrowhead inversion occurred followed by a steady climb until the end of the experiment. A second experiment using genotypes derived from this laboratory population after 26 generations, showed that the Arrowhead inversions had increased in adaptive value due to natural selection within the Arrowhead gene pool. It is this improvement that was responsible for the loss of the balanced polymorphism.

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NATURAL SELECTION IN WATER SNAKES (*NATRIX SIPEDON* L.) ON ISLANDS IN LAKE ERIE

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Although in recent years laboratory selection has become a commonplace, natural selection operating in wild populations has been quite difficult to document. Much of the published work has been inconclusive (see summary in Robson and Richards, 1936, for early work) or open to controversy (e.g., Lamotte, Cain and Sheppard, and Sedlmair on *Cepaea*). The present study analyzes all available data on color pattern variation in the water snakes of the Lake Erie islands. These data appear to illustrate a situation in which migration and strong selection pressure combine to give a relatively clear-cut picture of differential elimination of color pattern types from a population.

The uniform medium-gray color of the majority of adult water snakes inhabiting the islands in the western part of Lake Erie (as opposed to the "normal" dark banded type) was first noted by Morse (1904). In 1937 Conant and Clay described the island population as a separate subspecies *Natrix sipedon insularum,* differing from typical *sipedon* primarily in the large percentage of unbanded or weakly banded individuals. In 1954 Camin, Triplehorn and Walter compared the frequencies of various pattern types in wild-caught juveniles with those of the adult population and found a statistically significant decrease in the proportion of banded individuals from the juvenile to the adult population. In the present paper these previous data are reanalyzed and integrated with additional data, principally on frequencies of pattern types in litters, in order to present a picture of the entire post-natal selection for pattern type.

MATERIALS AND METHODS

Data from Middle Island are from the collections of Camin, Triplehorn and Walter made in 1949 and Camin and Ehrlich in 1957. Litter data from the Bass Complex islands are from the collections of Camin in 1948 and Camin and Ehrlich in 1957. All other data are from Conant and Clay (1937).

Conant and Clay originally divided the continuous variation in pattern types arbitrarily into four classes A–D (see figure 1), A being unbanded and D being typical banded *N. sipedon sipedon.* For greater precision, Camin *et al.* added the intermediate categories ab, bc and cd. These latter categories are employed here when comparison with Conant and Clay's data is not required. Where necessary for statistical tests, categories were lumped as follows: A = A + ab, B = B, C = bc + C, D = cd + D. A + B and C + D were lumped where the tests required only two classes of individuals. For convenience in the discussion to follow, "banded" and "unbanded" will be used to describe the two halves of the pattern spectrum (e.g., when referring to the effects of migration of "unbanded" individuals, we are including types ab and B snakes, which actually do show some light banding).

"Bass Complex" refers to North Bass, Middle Bass, South Bass, Green and Rattlesnake Islands. Middle-Pelee refers to Middle and Pelee Islands. "Peninsular mainland" refers to collections from Port

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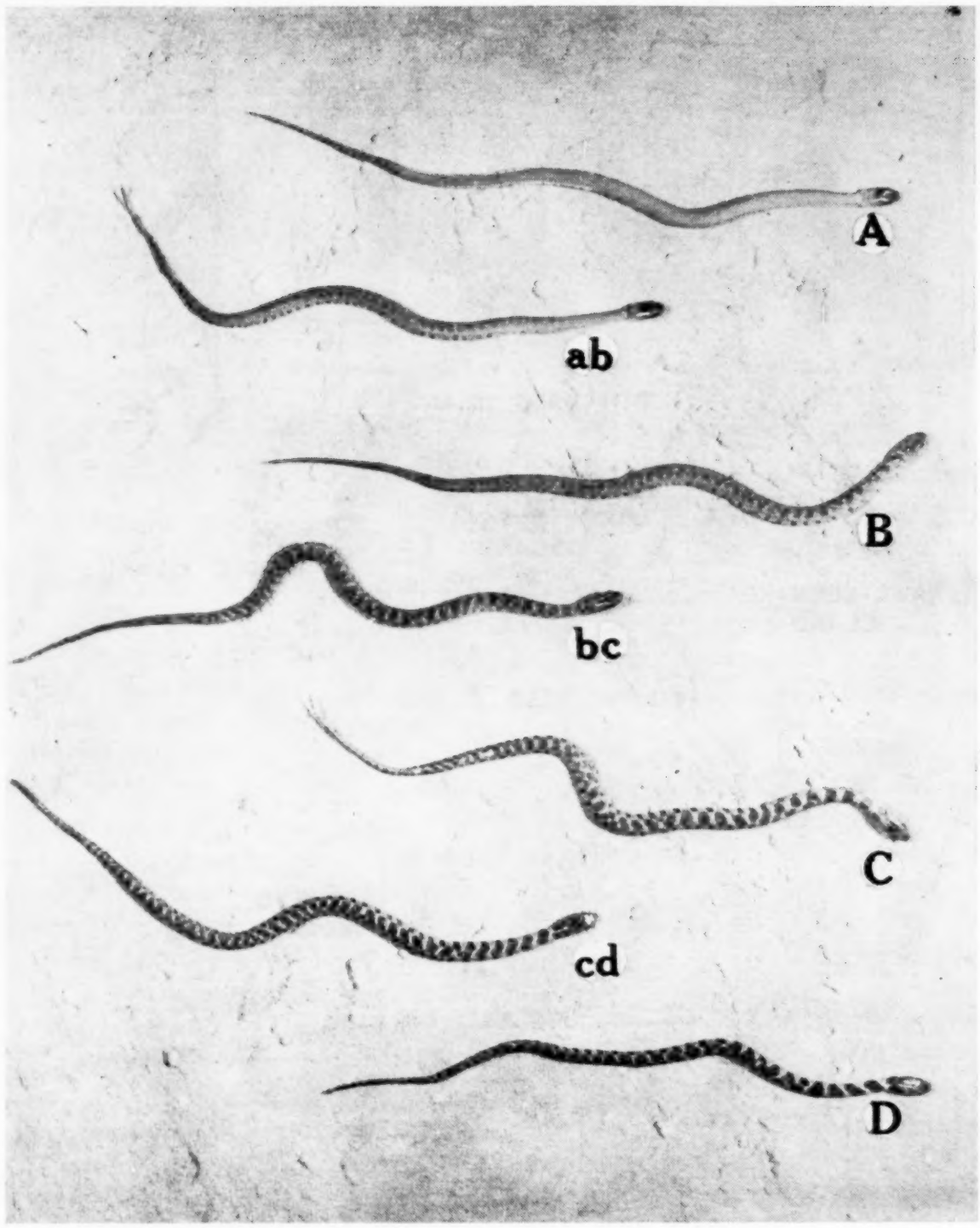

FIG. 1. Pattern types of island water snakes.

Clinton, Lakeside, Marblehead and Catawba Peninsula (all Ohio).

All pregnant females were isolated and their litters, including those stillborn, were scored as to pattern type. There was no sign of a correlation between pattern type and live birth.

There is no evidence that there is any change in pattern type from birth to maturity. Both Conant and Camin have kept individuals of *N. s insularum* in captivity over periods of several years without noticing any change in pattern. Individuals of all pattern types have been recorded from the adult population.

DESCRIPTION OF THE ISLANDS

The Lake Erie islands (fig. 2) vary in area from less than one acre to about fifteen square miles. The islands are wooded, and with a few exceptions (such as a large marsh on Middle Bass) they have little or no inland water. In general the water snakes are confined to the peripheries of the islands where they sub-

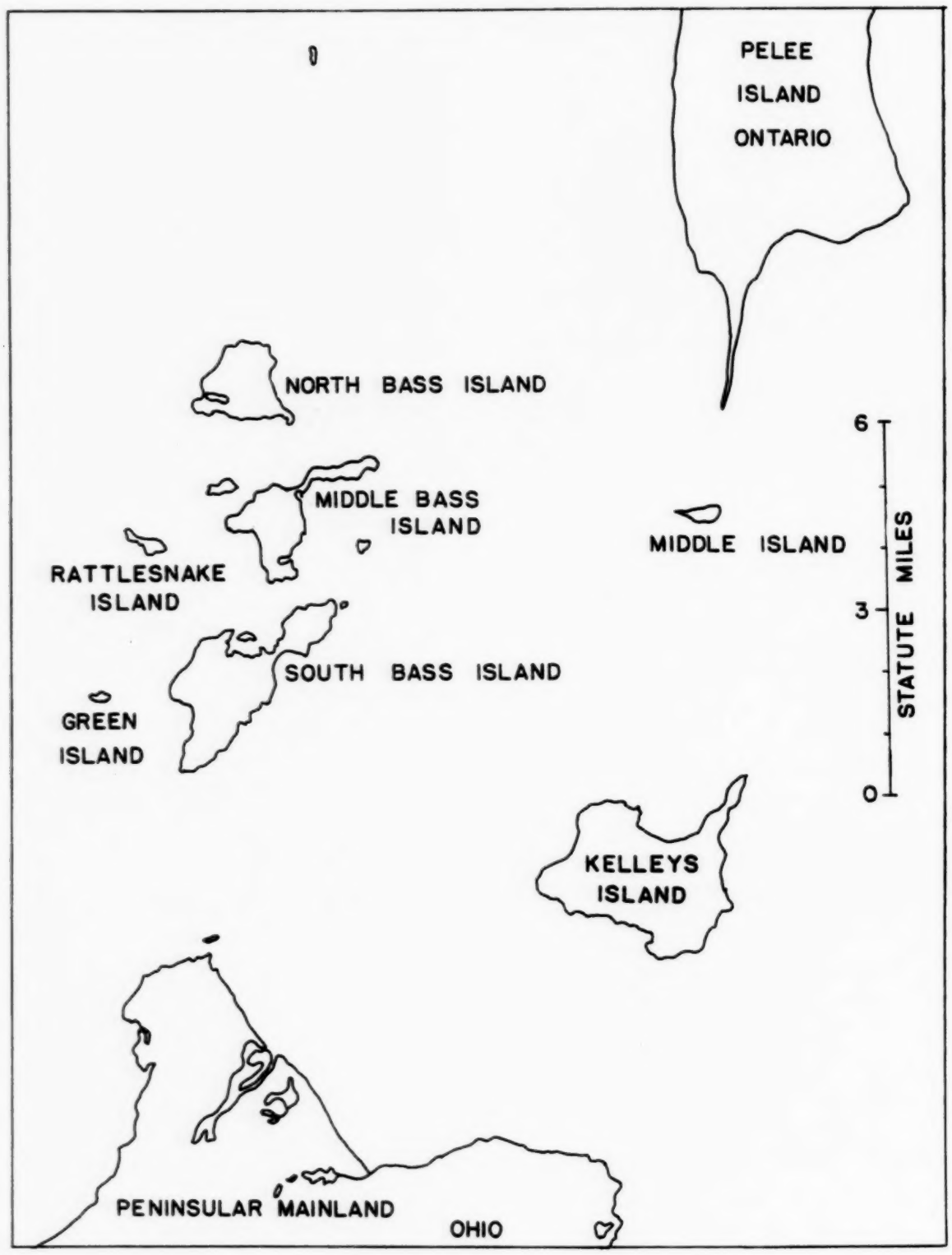

FIG. 2. Map of Lake Erie islands.

sist in large part on *Necturus* and storm-killed fish (Conant, 1951 and unpublished observations). The peripheries of the islands consist of flat limestone rocks (see Conant, 1951, Pl. 26, fig. 1), limestone cliffs or limestone pebble beaches.

The highest point on the islands is on South Bass (about 70 feet above lake level). Middle Island is approximately 15 feet above lake level at its highest.

GEOGRAPHIC VARIATION

As can be seen from the histograms (fig. 3), there is considerable geographic variation in pattern type. All the Ontario mainland snakes were typically banded *sipedon* and the peninsular mainland samples contained a very few unbanded individuals. The difference between the Ontario and Peninsular

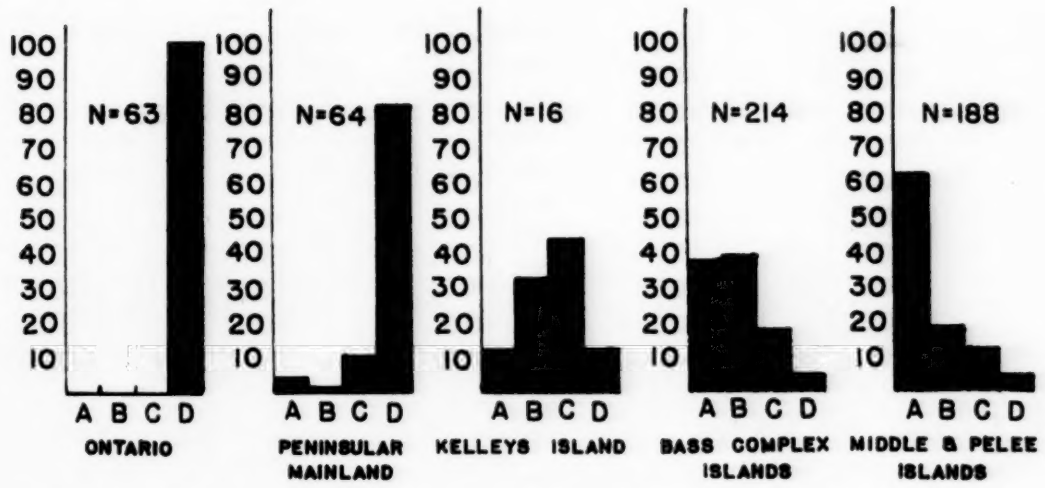

FIG. 3. Geographic variation (ordinates—per cent of total; abscissas—pattern types).

samples was not significant by Fisher's exact probability test ($P = .123$).

The sample from Kelleys I. contains a significantly greater proportion of banded individuals than that from the Bass Complex (chi-square, $.01 > P > .001$) and the Bass Complex sample has a significantly larger proportion of banded individuals than the one from Middle-Pelee (chi-square, $P << .001$).

Camin and other biologists in the area have frequently observed snakes swimming several miles from the nearest shore. This would indicate that there is considerable mainland-island and inter-island migration. A major factor in maintaining the geographic variation would appear to be this pattern of migration. Whereas South Bass and Kelleys Islands would probably receive about equal numbers of banded mainland migrants, South Bass doubtless receives additional migrants from the more northerly members of the Bass Complex. Because of their greater distance from shore, these northern islands of the Bass Complex would receive fewer typical *sipedon* migrants from the mainland and thus have populations with a lower proportion of banded individuals. The unbanded southward migrants could account for the fact that South Bass (as well as the Bass Complex as a whole) has a lower proportion of banded individuals than does Kelleys.

Similarly the relative isolation from the mainland of Middle and Pelee Islands could account for the greater proportions of unbanded individuals in their populations.

EVIDENCE OF SELECTIVE ELIMINATION

Figure 4 shows by histograms the pattern type frequencies of Bass Complex litters and adults and Middle Island litters, juveniles and adults.

The "raw" litter data are presented by histograms in figures 5 and 6. In these figures, the type classification of the female parent is indicated by a vertical line topped by the ♀ symbol. It is interesting to note that in all but one litter the female was of a class closer to the unbanded extreme of the distribution than was the median class of the offspring. A number of genetic explanations could account for this phenomenon, but without further data an hypothesis would have no value.

Because of the restrictions placed on the data by the fact that the litters are samples from the sample of the total gene pool carried by their parents (a type of cluster sampling), it is immediately apparent that simple chi-square analysis would not give a legitimate test of the apparent differences in type frequencies between the litter and adult populations. The young are not mutually independent samplings from the population of young, as the adults are from the adult population; on the contrary, phenotypes of dif-

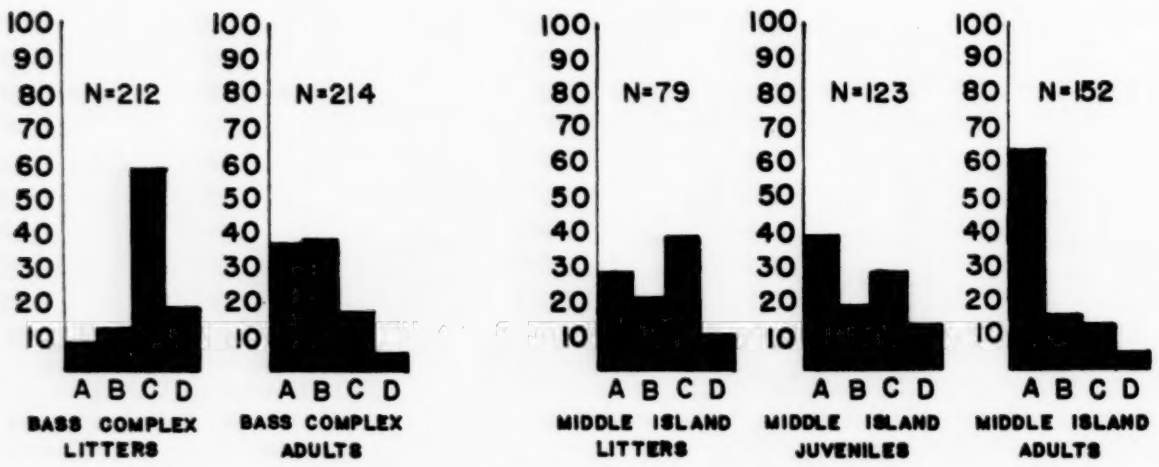

FIG. 4. Comparisons of young and adults (ordinates—per cent of total; abscissas—pattern types).

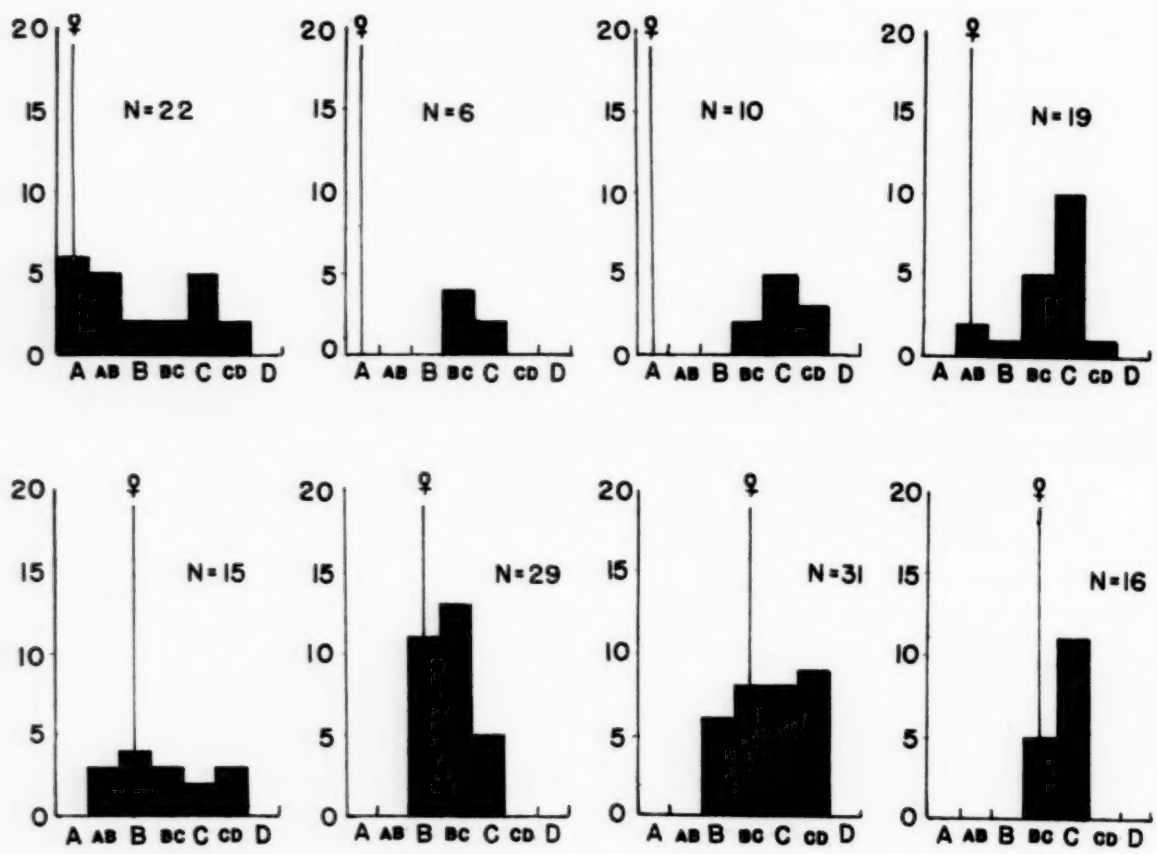

FIG. 5. Distribution of pattern types in Bass Complex litters (ordinates—number of individuals).

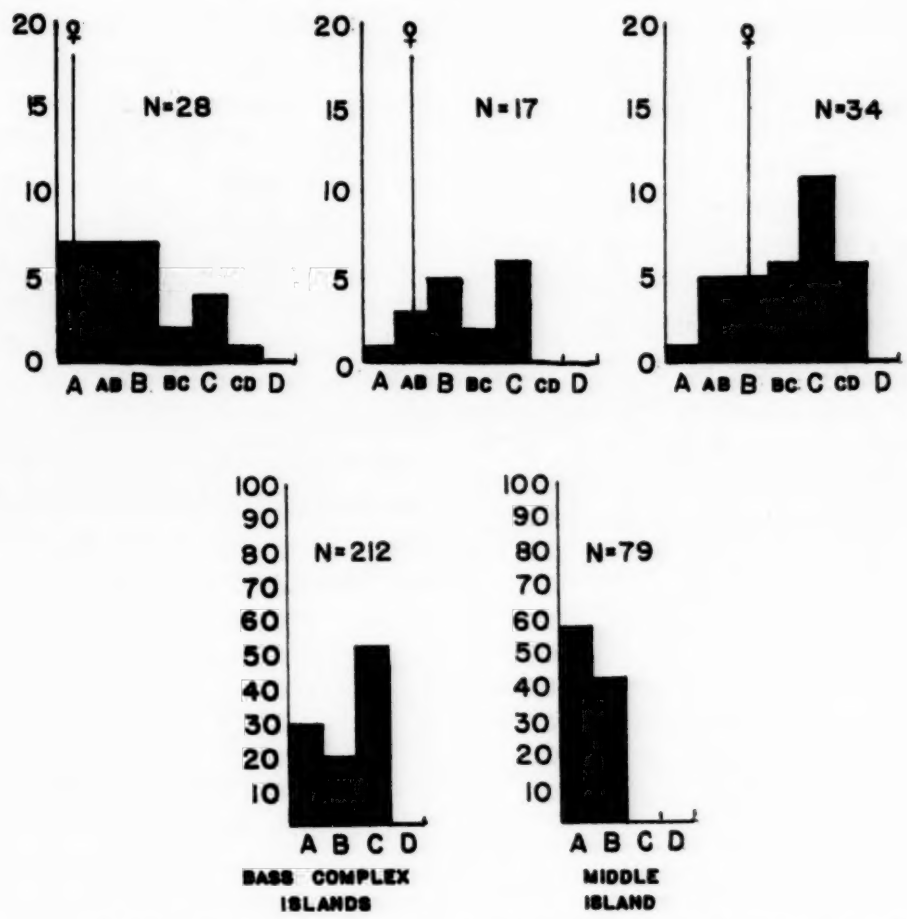

FIG. 6. 1st row: Distribution of pattern types in Middle Island litters (ordinates—number of individuals); 2nd row: Litters classified by female parent type (ordinates—per cent of total).

ferent individuals in the same litter present considerable correlation.

Using a formula[1] for the most conservative estimate of the variance of $\hat{p}$ (an estimate of the parametric proportion of types A + B) in the litter populations, and the binomial variance for the adult populations, the significance of the differences between the litter and adult populations was tested using the Fisher-Behrens test with infinite and 213 degrees of freedom. It was found that the Bass Complex litter population was significantly different ($P < .001$) from the Bass Complex adult population.

The Middle Island litter population was not found to be significantly different from the Middle Island adult population. This failure to demonstrate a statistically significant difference is doubtless due to the insufficient sampling (3 litters only) of the litter population, since the similarly constituted wild-caught juvenile population is significantly different from the adult population (chi-square; $P < .01$).

[1] Mr. David W. Calhoun, biometrician with G. D. Searle and Co., has contributed the following derivation: A simple upper limit for the variance of $\hat{p}$ can be obtained as follows. As a model let us assume each litter is associated with a probability, p, that any individual will be of type "A or B." The individuals making up a single litter form a binomial sample with parameter p. The values of p for different litters may be different, the distribution of these p's for the population of litters being unknown. Assume, finally, that litter size does not depend on p. Then the variance of $\hat{p}$, the proportion of type "A or B" in the pooled sample from all litters, has the form

$$\text{Var}(\hat{p}) = A\Sigma n^2/(\Sigma n)^2 + B/(\Sigma n)$$

where the n's are the individual litter sizes, A is the true variance (unknown) of the distribution of p's among litters and B is the average of the binomial variances pq for individual litters. Neither A nor B can exceed 0.25, and they cannot both assume this value, no matter what the distribution of p. Therefore

$$\text{Var}(\hat{p}) < 0.25[\Sigma n^2/(\Sigma n)^2 + 1/(\Sigma n)].$$

Discussion

The observed significant differences between the young and adult populations can only be accounted for by differential elimination of the banded pattern types or by pattern changes in the individual snakes. The evidence is overwhelmingly in favor of the former hypothesis.

There are a number of possible explanations for the presence of the unbanded populations on the Lake Erie islands. The environmental conditions of the islands might induce purely phenotypic changes in snakes which matured there. The fact that the unbanded pattern types are found in the litters, and the evidence indicating no change in pattern type of individual snakes throughout life would seem to obviate this possibility.

A high proportion of unbanded pattern types might be maintained by migration from other unbanded populations. However, all known *N. sipedon* populations that could possibly supply migrants are made up of typical banded snakes.

For the frequency of unbanded genotype to be maintained by mutation alone in the observed populations would require directed mutation at a rate far above that known for any locus ever studied in any organism, even if it is assumed that color pattern is a single factor trait.

Genetic drift is not indicated as a factor in maintaining the high frequency of unbanded individuals on the islands for two reasons: First, the snakes are extremely abundant on the islands (seven collectors captured about 400 *N. sipedon* on Middle Island in five hours in 1949; three collectors captured 234 in four hours on South Bass in 1935) so that there is no reason to believe that their effective population size on any of the larger islands would approach the level at which drift would be an important factor. Second, the pattern trend is towards unbanded individuals on all the islands, which indicates a systematic pressure rather than random drift.

Therefore, by a process of elimination, selection alone can reasonably account for the presence of populations with a high proportion of unbanded individuals on the islands.

Although it is not essential to the case in point, the source of the selection pressure is of considerable interest. To the human eye, the unbanded snakes are very effectively cryptically colored when they are on the flat limestone rocks of the island peripheries. In contrast, the banded individuals are highly conspicuous. It seems likely that a visual predator is one of the principal selective influences. Gulls are abundant around the islands and experiments by the authors (carried on with the cooperation of the Lincoln Park Zoo) indicated that gulls would eat young water snakes. Other likely predators are herons (which are abundant in the area), raptors, and (recently) man.

Whatever the selective agents are, it appears that the establishment of a genetic system producing essentially 100% unbanded individuals has been prevented by a continual influx of "banded" genes brought into the island gene pools by a steady flow of mainland immigrants. This balance between strong selection and migration pressures has produced a situation which lends itself extraordinarily well to analysis. Unfortunately the presence of some migrant individuals makes it impossible to determine the exact composition of the non-migrant (selected) adult population.

On examining the works of Conant and Clay (1937) and Conant (1951) it becomes apparent that, in the problem at hand, the subspecies approach has tended to obscure a significant biological problem. Snakes of intermediate pattern types were considered to be intergrades between two distinct biological entities and some of the dynamic aspects of the situation were not considered. This should not be construed as criticism of Conant and Clay, whose careful and de-

tailed analysis has made possible the present study.

It should be noted that as long ago as 1942, Dunn pointed out the value of snakes and other reptiles for studies of selection in operation. It is hoped that this line of investigation will not continue to be neglected.

Summary

Data are presented indicating postnatal selection for pattern type in water snakes (*Natrix sipedon*) on the islands of Lake Erie. Strong selection, demonstrable without regard to selective agent, has produced a shift towards unbanded pattern types on the islands, while constant migration from the mainland has maintained "banded" genes in the island gene pools. These antagonistic pressures have produced a situation unusually amenable to analysis.

Acknowledgments

We wish to thank the following individuals for aid on various aspects of the work: David W. Calhoun, Skokie, Illinois; Roger Conant, Philadelphia Zoological Garden; Henry S. Dybas, Chicago Natural History Museum; Howard K. Gloyd, Chicago Academy of Sciences; Robert W. Hull, Northwestern University; Ernst Mayr, Harvard University; R. Marlin Perkins, Lincoln Park Zoo, Chicago; Loren S. Putnam, Ohio State University; George B. Rabb, Brookfield Zoological Garden, Brookfield, Illinois; and Edward S. Thomas, Ohio State Museum. We would also like to acknowledge the assistance of our wives, Emily F. Camin and Anne H. Ehrlich, in the preparation of the manuscript and figures.

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[2] These references selected from the extensive literature on the question of selection in *Cepaea*.

A CONSPECTUS OF HYBRIDIZATION IN THE ORCHIDACEAE

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Since the mid-nineteenth century [2] when the first orchid hybrid of artificial origin was produced, more than 10,000 primary [3] hybrids have been officially registered. Many of them and their parental species have been illustrated in detail in various specialized publications. Taken as a whole this constitutes one of the world's largest reservoirs of codified facts relating to inter-specific and intergeneric hybridization. Because of their beauty, rarity, and complexity, orchids have exercised a special fascination for many people in many countries. Just as popular interest has advanced our understanding of speciation in birds (Mayr, 1942, p. 5) over that of all other vertebrates, so popular interest in the Orchidaceae has put them in a favored position with regard to monographs, living collections, publication of colored illustrations, production of artificial hybrids, and registration of seedlings.

Because of the specialized nature of orchid growing and orchid hybridizing and of the monetary value of many of the hybrids, their pedigrees have been more carefully supervised and officially recorded than have those of any other large group of plants. These official records are of the same order of accuracy as those for blooded stock and are subject to the same sorts of wilful and accidental error. The most important sources of information concerning pedigrees are Rolfe and Hurst (1909), and Sanders (1946, 1949, 1952, 1955).[4]

Now that we are moving rapidly towards an appreciation of such facts and an increased understanding of their significance for theories of evolution (Anderson and Stebbins, 1954), it seems appropriate to call attention to this corpus of pertinent data and to give the briefest possible summary of its extent and its bearing on evolutionary problems.

Before we can present the data we must come to some kind of decision about the generic problem in orchids. The only course open to us is to take, as a rough operational definition, those genera of orchids commonly accepted as such. Some of them are certainly of the same taxonomic significance as genera in other families of plants and animals. As in many other families, some of the genera will suffer drastic overhauling when combined morphological, distributional, genetical and cytological information is brought to the problem by skilled monographers. Any of the crosses catalogued as intergeneric must at the very least represent crosses between distinct species groups; few, if any, are between taxa as closely related as two well-established geographical sub-species of the higher vertebrates.

In one respect the official record of registered crosses gives us a one-sided picture of hybridization in the Orchidaceae. It tells us nothing about the crosses which were attempted and did

[1] Part of the expense entailed in preparing this paper for publication was met from a grant-in-aid to the junior author by the National Science Foundation for studies in hybridization.

[2] Orchid Review, **1**: 3–6, 1893.

[3] Primary hybrids are those in which neither parent is itself a recognized hybrid.

[4] L. W. Lenz and D. E. Wimber have prepared a general review of hybridization and inheritance for the comprehensive "Manual of Orchidology," now in press.

not succeed. It is well known to orchid hybridizers that many crosses (even those between species of the same genus) are impossible to make by any ordinary methods. For Odontoglossum, for instance, there are no records of hybrids between species in certain sections. In response to an inquiry for more definite information, one able and experienced orchid hybridizer, Oscar Kirsch, wrote us as follows:

"It is, of course, a well-known fact that Dendrobiums will only cross within their own closely circumscribed groups. To prove the rule, a few exceptions are known and maybe more knowledge of their make-up is needed. We have tried many times to cross members of the nobile type of Dendrobium with members of the antelope and *Dendrobium phalaenopsis* types. We have never succeeded. I have heard of a few instances claimed, but have never seen any of the products that would convince me that the claims are worth considering. The same goes for combinations of the Indian yellow types, such as aggregatum, farmeri, dalhousieanum, etc. They again have been disappointments, although again a few instances have been cited where they have entered into combinations with other groups. The list of orchid hybrids contains a number of instances where crosses are registered as having produced offspring that are considered impossible. One classic example is *Den. Kukui*. *Den. Kukui* is registered as a hybrid of *Dendrobium phalaenopsis* × *Den. moschatum* var. *cupereum*. The actual parentage unquestionably is *Den. phal.* × *Den. undulatum*, which is registered as *Den. Pauline*. However, somehow or other the cross was "accepted" and registered and has since produced any number of new hybrids which, of course, are equally erroneous. This instance ought to be sufficient proof that we can't accept everything we read in the list of orchid hybrids as the gospel truth. There is, however, so far no accepted international machinery which could be used to eliminate such errors."

This is a difficult subject on which to get really accurate information since the terms fertility and sterility are comparative rather than absolute. When we say that it is impossible to cross two species and obtain hybrids do we mean ten times out of ten or 10^8 times out of 10^8? Such modern studies as those of Venkatraman (1932, 1937) and Janaki-Ammal (1941, 1942) demonstrate that hybrids previously considered outside the range of possibility can be produced readily when the attempt is made with much larger numbers.

Table 1 lists by genera the number of different primary hybrids which had been registered up to 1947. It will be seen that about one in ten of these hybrids were collected in the wild; the others were grown in cultivation, most of them from controlled pollinations. Most of the putative hybrids collected in the wild have had experimental confirmation since they were described; few, if any, of them were acknowledged as hybrids until confirmed by controlled crosses. For the most commonly cultivated orchids such as the Cypripedileae, the genera Cattleya, Dendrobium, Odontoglossum and Vanda, the

TABLE 1. *List of number of registered interspecific primary hybrids by genera*

Aerides, 1871*, 2; Angraecum, 1899, 2 (1 natural hybrid); Anguloa, 1881, 4 (1 natural hybrid); Anoectochilus, 1865, 1; Arachnis, 1940, 3; Brassavola, 1938, 2; Bulbophyllum, 1937, 1; Calanthe, 1852, 7; Catesetum, 1 (natural hybrid); Cattleya, 1859, 264 (26 natural hybrids); Chysis, 1874, 3; Cirrhopetalum, 1936, 2; Cochlioda, 2 (2 natural hybrids); Coelogyne, 1906, 9; Cymbidium, 1889,† 33 (7 natural hybrids); Cynorchis, 1903, 1; Cypripedium (Paphiopedilum), 1869, 333 (7 natural hybrids); Dendrobium, 1849, 118 (14 natural hybrids); Disa, 1891, 11; Epidendrum, 1888, 22; Eulophiella, 1917, 1; Habenaria, 1910, 4 (1 natural hybrid); Laelia, 1864, 59 (6 natural hybrids); Masdevallia, 1880, 39 (1 natural hybrid); Maxillaria, 1930, 1; Miltonia, 1889, 12 (9 natural hybrids); Odontoglossum, 1896, 193 (41 natural hybrids); Oncidium, 1909, 37 (8 natural hybrids); Phaius, 1891, 13; Phalaenopsis, 1886, 41 (9 natural hybrids); Promenaea, 1905, 2; Renanthera, 1942, 3; Saccolabium, 1 (natural hybrid); Selenipedium (Phragmipedium), 1870, 18; Sobralia, 1895, 9; Spathoglottis, 1897, 16 (1 natural hybrid); Stanhopea, 1890, 7 (1 natural hybrid); Thunia, 1885, 2; Trichopilia, 1911, 1; Vanda, 1914, 75 (4 natural hybrids); Zygopetalum, 1877, 12.

* First registration date.

† In spite of the large number of named varieties of Cymbidiums only 2 primary hybrids were registered before 1900.

TABLE 2. *List of registered inter-generic primary hybrids*

Adaglossum, Ada × Odontoglossum, 1913,† 3; Adioda, Ada × Cochlioda, 1911, 1; Aeridachnis, Aerides × Arachnis, 1957; Aeridopsis, Aerides × Phalaenopsis, 1918, 1; Aeridovanda, Aerides × Vanda, 1918, 8; Angulocaste, Anguloa × Lycaste, 1903, 6; Anoectomaria, Anoectochilus × Haemaria, 1865, 1; Arachnopsis, Arachnis × Phalaenopsis, 1941, 2; Aranda, Arachnis × Vanda, before 1937, 23; Aranthera, Arachnis × Renanthera, 1937, 7; Ascocenda,** Ascocentrum × Vanda, 1949, 3; Brassidium,* Brassia × Oncidium, 1948, 1; Brassocattleya, Brassavola × Cattleya, 1869,†† 57; Brassodiacrium, Brassavola × Diacrium, 1909, 1; Brassoepidendrum, Brassavola × Epidendrum, 1906, 2; Brassolaelia, Brassavola × Laelia, 1898, 14; Cattletonia, Broughtonia × Cattleya, 1957; Chondrobollea, Chondrorhyncha × Bollea, no date, 1†††; Chondropetalum, Chondrorhyncha × Zygopetalum, 1908, 1; Diabroughtonia, Broughtonia × Diacrium, 1956; Diacattleya, Diacrium × Cattleya, 1908, 3; Dialaelia, Diacrium × Laelia, 1905, 2; Dossinimaria, Dossinia × Haemaria, 1861, 1; Epicattleya, Epidendrum × Cattleya, 1897, 24; Epidiacrium, Epidendrum × Diacrium, 1905, 3; Epigoa, Domingoa × Epidendrum, 1957; Epilaelia, Epidendrum × Laelia, 1894, 20; Epiphronitis, Epidendrum × Sophronitis, 1890, 2; Laeliocattleya, Laelia × Cattleya, 1863, 265; Laelonia, Laelia × Broughtonia, 1957; Leptolaelia, Laelia × Leptotes, 1902, 1; Luisanda,*** Luisia × Vanda, 1952, 1; Lycasteria,*** Bifrenaria × Lycaste, 1954, 1; Macomaria, Macodes × Haemaria, 1862, 1; Miltonioda, Miltonia × Cochlioda, 1909, 5; Miltonidium, Miltonia × Oncidium, 1940, 2; Odontioda, Odontoglossum × Cochlioda, 1904, 42; Odontocidium, Oncidium × Odontoglossum, 1911, 14; Odontonia, Miltonia × Odontoglossum, 1905, 20; Oncidioda, Oncidium × Cochlioda, 1910, 17; Opsisanda,* Vanda × Vandopsis, 1947, 2; Phaiocalanthe, Phaius × Calanthe, 1867, 2; Phaiocymbidium, Phaius × Cymbidium, 1902, 1; Renades, Renanthera × Aerides, 1955; Renanopsis,* Vandopsis × Renanthera, 1948, 1; Renantanda, Renanthera × Vanda, 1935, 17; Renanthopsis, Phalaenopsis × Renanthera, 1931, 5; Rodricidium, Oncidium × Rodriguezia, 1957; Sarcothera,*** Sarcochilus × Renanthera, 1954, 1; Schombocattleya, Schomburgkia × Cattleya, 1903, 1; Schomboepidendrum, Epidendrum × Schomburgkia, 1957; Schombolaelia, Schomburgkia × Laelia, 1913, 1; Sophrocattleya, Sophronitis × Cattleya, 1886, 19; Sophrolaelia, Sophronitis × Laelia, 1894, 11; Staurachnis,** Stauropsis × Arachnis, 1950, 1; Tricocidium, Oncidium × Trichocentrum, 1955; Tricovanda,* Tricoglottis × Vanda, 1948, 1; Vandachnis,** Vandopsis × Arachnis, 1948, 1; Vandaenopsis, Vanda × Phalaenopsis, 1931, 13; Zygobatemannia, Zygopetalum × Batemannia, 1899, 1; Zygocaste, Zygopetalum × Lycaste, 1945, 1; Zygocolax, Zygopetalum × Colax, 1886, 6; Zygonisia, Zygopetalum × Aganisia, 1902, 2.

* Generic name appearing first in Sanders' Hybrid List Addendum 1946–1948.
** Generic name appearing first in Sanders' Hybrid List Addendum 1949–1951.
*** Generic name appearing first in Sanders' Hybrid List Addendum 1952–1954.
† First registration date.
†† Only 3 before 1900.
††† Natural hybrid.

number of registered secondary hybrids exceeds almost ten-fold the number of primary hybrids and the proportion as well as the number of such secondary hybrids is very much on the increase.

In table 2 are listed 63 inter-generic primary hybrids. Since by definition no tri-generic hybrid could be a primary hybrid, we have summarized in table 3 *all* registered hybrids involving three genera. There are, in addition, two sets of hybrids involving four genera and these are listed in Table 4.

As can be seen from inspection of tables 2 and 3 most of these intergeneric hybrids fall into five groups. The three largest of these groups are diagrammed in figures 1, 2 and 3 which show all the combinations involving two genera which have been registered for each group and give a rough indication of the number of crosses between each pair of genera. For the total number of genera involved, the Vanda group leads with 11 genera. For the total number of registered intergeneric crosses the Cattleya group leads with over 5000!

Scientists who have worked with other groups of organisms (particularly with those which cannot be bred in cap-

tivity with something like normal vigor) will tend to be skeptical of these data. They will attempt to harmonize them with their own experience by suggesting that the orchid genera involved cannot possibly be "good genera." It is certainly true that the genera in these groups (as in many other families of plants and animals) are in need of careful revision. It is doubtful, for instance, if the differences between Cattleya and its allied genera have been established on natural lines. However, unless by fiat in advance of the experimental evidence, one rules that no cross yielding semi-fertile progeny is possible between "good genera," some of the genera involved would pass most ordinary criteria. In the Miltonia crosses the flowers differ in size, texture, color, and proportion. The lip petals in the different genera involved in the tri-generic hybrid Vuylstekeara are so variously differentiated by calluses and convolutions that it is difficult to be certain which parts of each flower are strictly homologous. This is shown even more strikingly in the hybrid between Zygopetalum and Colax. Detailed histological studies would increase rather than decrease the apparent differences between them. As a demonstration of strikingly different species which can be crossed and yield partially fertile progeny, figure 4 presents some kind of limiting case. Those who are interested in theories of speciation and evolution would do well to look into these facts. By any ordinary standards of morphology, geographical distribution, and the like, *Cochlioda noezliana*, *Miltonia vexillaria* and *Odontoglossum harryanum* belong to three highly differentiated species groups, they must at least be placed in sub-genera.

If we attempt to generalize from our knowledge of the Orchidaceae as to the prevalence and importance of hybridization there is one fact which is particularly disturbing—for no other family of plants or animals has there been such a concerted attempt to bring the rarest species together in cultivation, to make hybrids, and to grow hybrid seed in quantity. The mere raising of orchid seedlings was so difficult that not until laboratory techniques were available was it practicable to raise any considerable number to flowering size; now by the use of artificial media and laboratory methods, seedlings of many genera are raised to maturity by the hundreds of thousands annually. In other words if the Orchidaceae had been just as they are but had all their blooms been so tiny that their interest and beauty were not apparent to the naked eye, we would today know little or nothing about the frequency with which distinct species groups can be hybridized. The Podostemonaceae, for instance, have flowers and inflorescences quite as diverse and fascinating as those of the Orchidaceae but they cannot be appreciated without at least a hand lens. So far as I am aware

TABLE 3. *List of tri-generic hybrids*

Brassolaeliocattleya	Brassavola × Cattleya × Laelia	1897	1000+
Charlesworthеara	Cochlioda × Miltonia × Oncidium	1919	15
Dekensara	Brassavola × Cattleya × Schomburgkia	1955	
Dialaeliocattleya	Diacrium × Cattleya × Laelia	1908	2
Lowiara	Brassavola × Laelia × Sophronitis	1912	2
Rolfeara	Brassavola × Cattleya × Sophronitis	1919	16
Sanderara	Brassia × Cochlioda × Odontoglossum	1937	1
Sophrolaeliocattleya	Cattleya × Laelia × Sophronitis	1909	426
Tanakara*	Aerides × Vanda × Phalaenopsis	1951	1
Vuylstekeara	Cochlioda × Miltonia × Odontoglossum	1912	163
Wilsonara	Cochlioda × Odontoglossum × Oncidium	1916	16

* See note, table II.

TABLE 4. *List of tetra-generic hybrids*

Burrageara	Cochlioda × Miltonia × Odontoglossum × Oncidium	1927	2
Potinara	Brassavola × Cattleya × Laelia × Sophronitis	1922	62

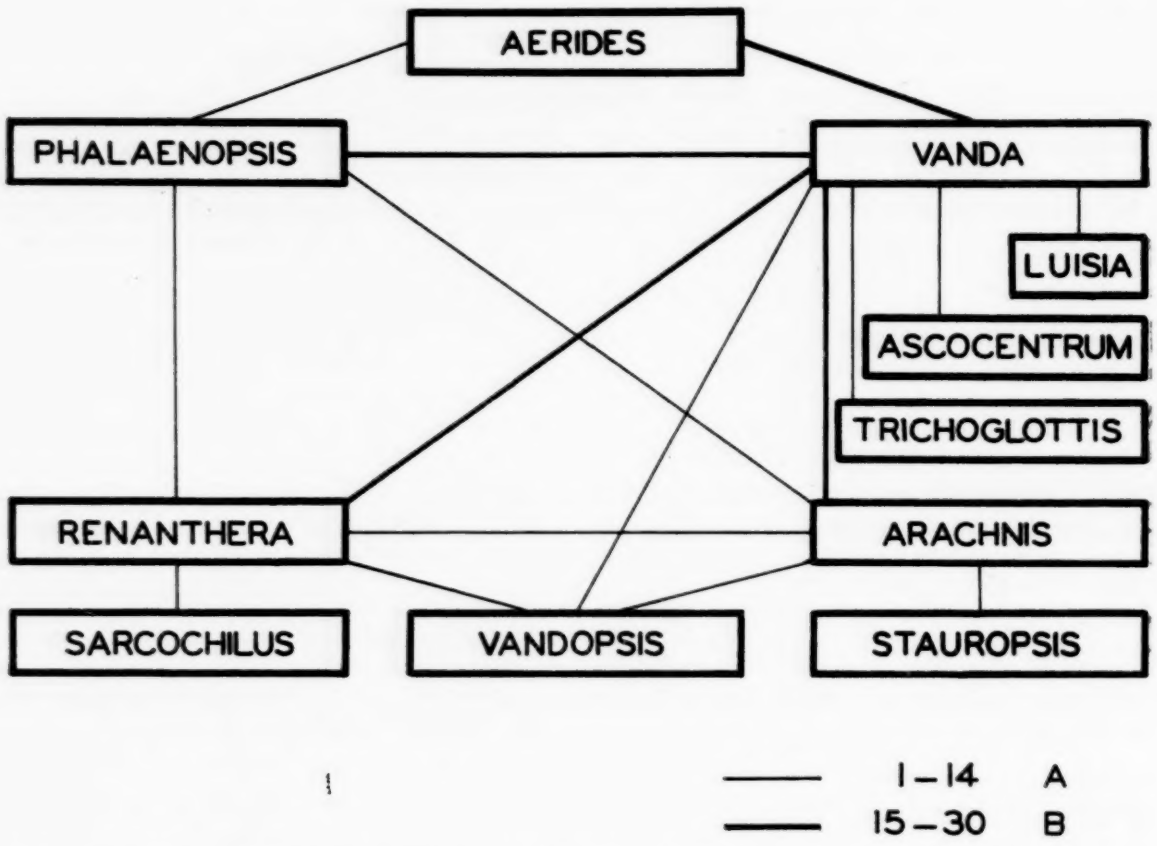

FIG. 1. Inter-generic crosses involving Vanda and related genera. Each line represents at least one hybrid. Width of line (as indicated to the right at the base) is proportional to the number of known hybrids.

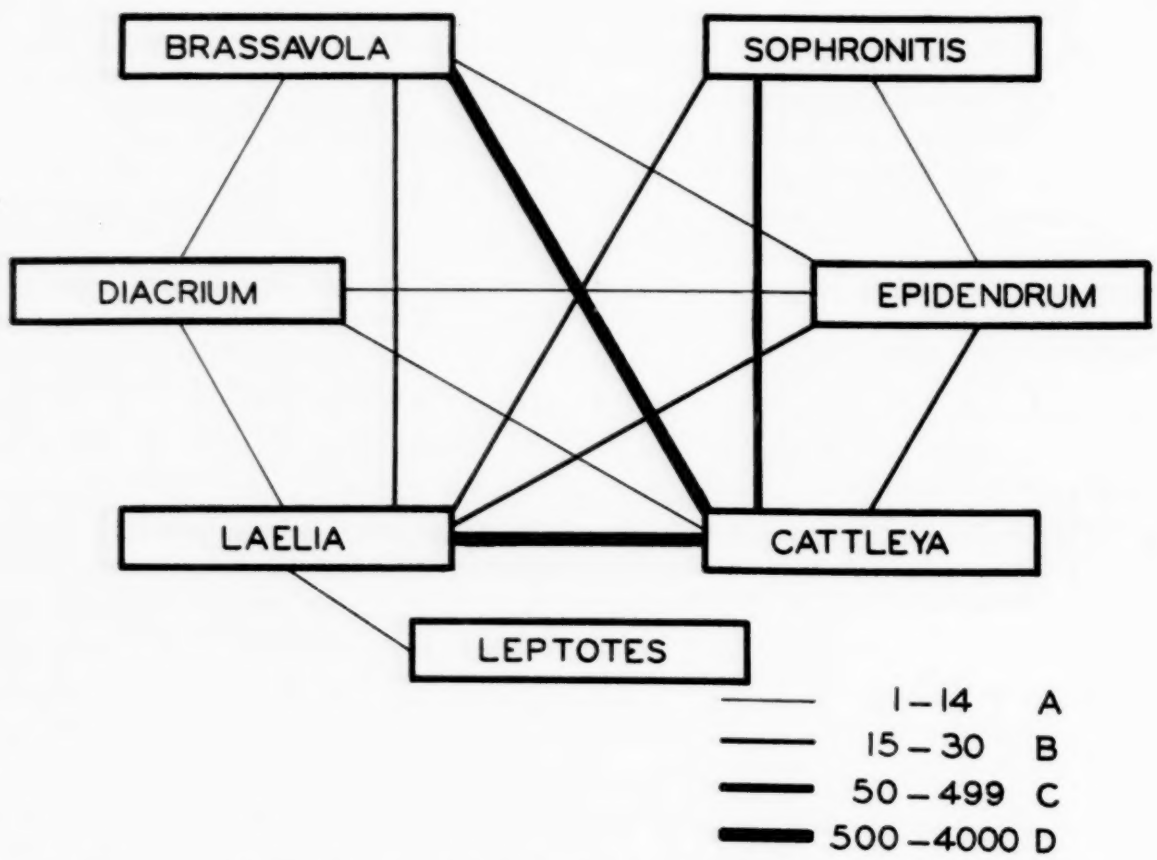

FIG. 2. Inter-generic crosses involving Cattleya and related genera. Width of line (as indicated to the right at the base) is proportional to the number of known hybrids.

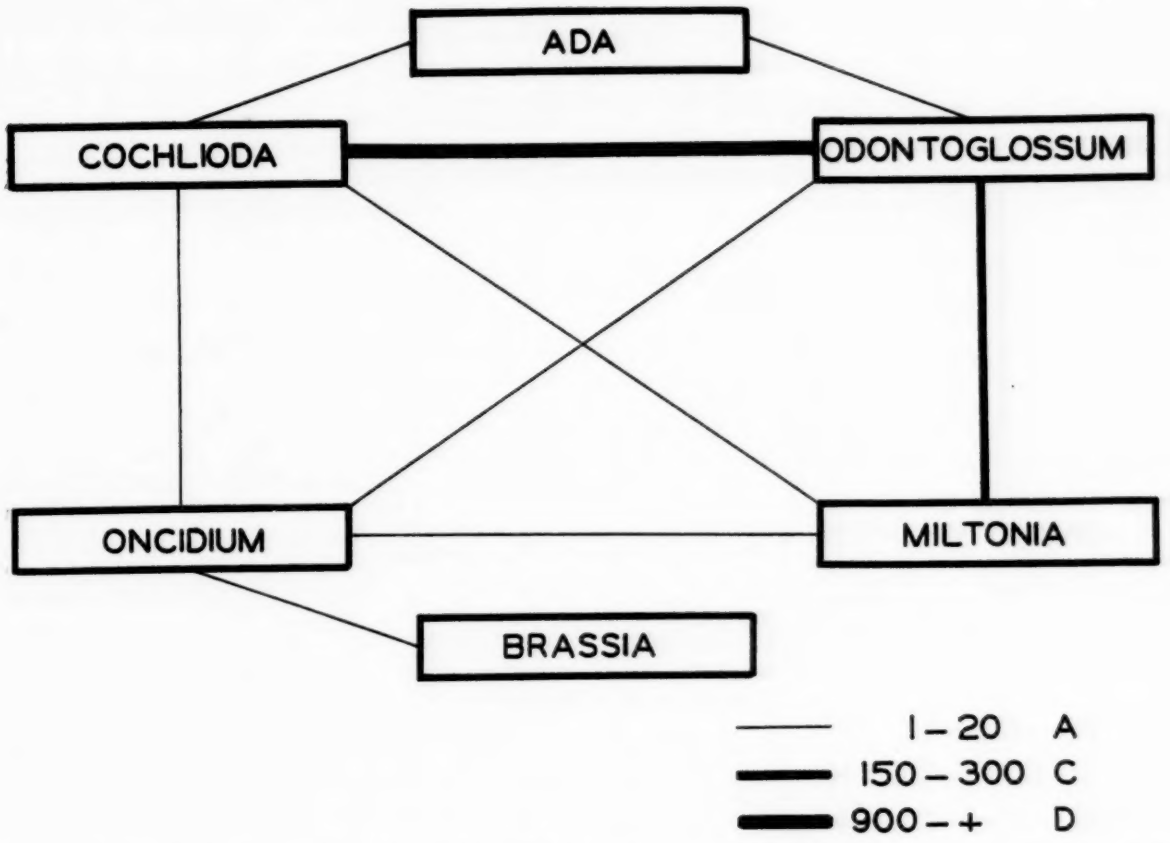

FIG. 3. Inter-generic crosses involving Odontoglossum and related genera. Width of line (as indicated to the right at the base) is proportional to the number of known hybrids.

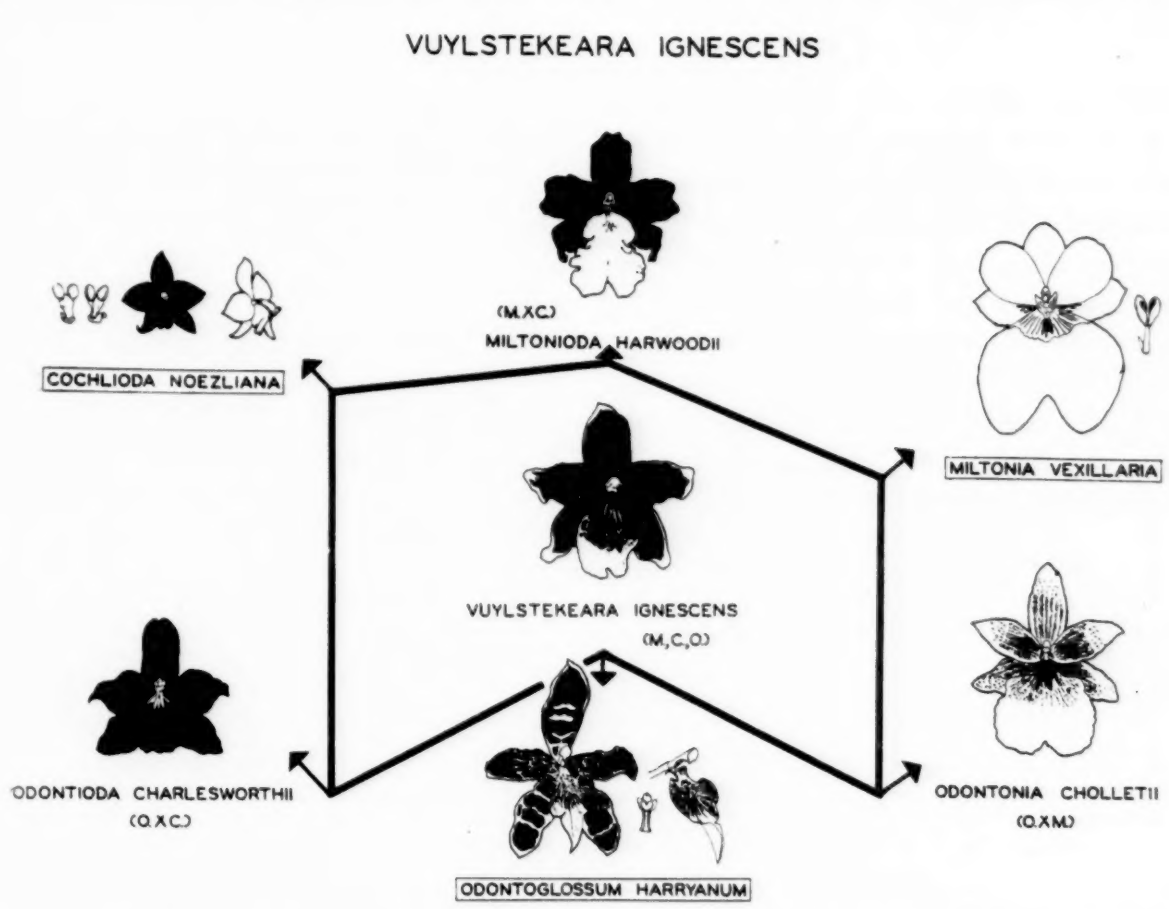

FIG. 4. The three species (belonging to the genera Miltonia, Odontoglossum and Cochlioda) from whose primary hybrids have been bred the tri-generic hybrids classified in the genus Vuylstekeara. One of these tri-generic hybrids is illustrated in the middle of the figure, the three original species are shown at the right and left above and the center below, their names surrounded by narrow lines. For the three primary hybrids, the genera from which they came are indicated within parentheses by their initial letters, M., C., and O.

there have been no attempts to hybridize them. If they were to be grown as skillfully and in as large quantities by as many people in as many countries as have the Orchidaceae, what would we know about *their* ability to hybridize?

Biologists concerned with the importance of hybridization, if they think about the Orchidaceae at all, usually think of them as a sort of limiting case of hybridization. They are even more strikingly a limiting case for the time, effort and scientific research which have been put into assembling collections and raising hybrids. In part, at least, the first limiting case must be a function of the second. If hybrid hummingbirds, for instance, were bred in captivity by the actual millions (as are orchids today) [5] what would we find out as to the frequency with which they can be hybridized and the probable phylogenetic consequences of hybridization in that group of animals?

Summary

More time, money, and scientific effort have gone into bringing into successful cultivation an important fraction of the Orchidaceae of the world than has been devoted to any other family of plants or animals. In the last century and a half, tens of thousands of crosses between species and some thousands of crosses between genera have been officially registered. Though well known to horticulturists, the extent of this record is realized by few biologists. It is here tabulated, one set of trigeneric hybrids are illustrated as an example, and the bearing of these data on evolutionary theories is briefly discussed.

[5] It is a reliable estimate that a single California commercial firm is today raising more than 200,000 hybrid seedlings at any one time.

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EYE PIGMENT RELATIONSHIPS IN THREE SPECIES GROUPS OF DROSOPHILA

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INTRODUCTION

The system of pigment cells in the compound eyes of *Drosophila melanogaster* has been described by Nolte (1950), Gersh (1952) and Clayton (1952). In these cells the pigment granules are laid down and they carry deposits of two pigment components, a red and a brown. These pigments can be extracted differentially (Ephrussi and Herold, 1944; Nolte, 1952); the red pigment is extracted in an acidified ethyl alcohol (AEA) and the brown pigment in acidified methyl alcohol (AMA). Quantitative estimations of the two pigments have been made by means of spectrophotometric analysis of the two extracts, and a comparison has been made between the wild type and a large number of mutant strains (Nolte, 1952–1955).

In a later study (Nolte, 1958b) the degree of dominance of wild type alleles of various mutant eye-color genes was investigated, and quantitative data were included for two South African strains of *D. melanogaster;* these were found to differ greatly from the data for the Canton-S strain which had mainly been used as a basis for the quantitative comparison of mutant strains of this species. This fact led to a consideration of the status of this quantitative characteristic in the various species and strains of *Drosophila* in South Africa. Since it then appeared that these pigment measurements might be useful characters for the analysis of natural populations, and could possibly be of interest in the tracing of phylogenies, the investigation was extended to include foreign species and strains. Since it is possible that the melanogaster and willistoni species groups are directly derived from the obscura group (Sturtevant, 1940), the investigation was extended to include species and mutant strains of these three groups of the subgenus Sophophora.

MATERIAL AND METHODS

The melanogaster group consisted of South African strains of *D. melanogaster, D. simulans, D. séguyi* (Burla, 1954) and *D. opisthomelaina* (Nolte and Stoch, 1950). The latter species has later been described as *D. yakuba* (Burla, 1954). For purposes of comparison two American strains of *D. melanogaster,* i.e., Canton-S and Oregon-R, were included in this study. The designations of the South African strains are given in table 1, together with the place and year of collection. Most of these strains were derived from several females but have been inbred since the time of collection. The geographic distribution of these strains is indicated in figure 1.

The willistoni group consisted of three Brazilian species, *D. willistoni, D. nebulosa* and *D. capricorni,* the designations of the strains being given in table 3.

The obscura group consisted of three North American species, *D. pseudoobscura, D. persimilis* and *D. miranda,* and some mutant eye-color strains of these species, the designations being given in table 4.

The methods applied in this study were similar to those of previous investigations (Nolte, 1952–1955) and consisted of the histological examination of the eye pigment cells, the differential extraction of the two pigments, their spectrophotometric analysis, and their photometric quantitative estimation.

TABLE 1. *The strains of the four South African species*

Strain	Collection year	Locality
D. melanogaster		
Cape Town—1	1948	Domestic
Stellenbosch—1	1947	Deciduous fruit orchard
Stellenbosch—2	1954	Deciduous fruit orchard
Graaff-Reinet—1	1949	Domestic
Graaff-Reinet—2	1949	Domestic
Cedara—1	1947	Domestic
Cedara—2	1947	Domestic
Witwatersrand—1	1947	Domestic
Witwatersrand—2	1944	Domestic
Witwatersrand—3	1950	Domestic
Nelspruit—1	1947	Subtropical fruit plantation
Nelspruit—2	1947	Subtropical fruit plantation
Nelspruit—3	1950	Subtropical fruit plantation
Inhaca—1	1947	Domestic, on Island
Inhaca—2	1947	Domestic, on Island
Inhaca—3	1953	Domestic, on Island
Inhaca—4	1954	Domestic, on Island
Inhaca—5	1955	Domestic, on Island
Zoutpansberg—1	1947	Citrus plantation
Zoutpansberg—2	1947	Citrus plantation
Zoutpansberg—3	1947	Citrus plantation
Zoutpansberg—4	1947	Citrus plantation
Limpopo—1	1957	Rubbish dump in camp
D. simulans		
Stellenbosch—3	1954	Deciduous fruit orchard
Witwatersrand—4	1944	Domestic
Witwatersrand—5	1950	Domestic
Witwatersrand—6	1955	Domestic
Mkuzi—1	1947	Game Reserve
Zoutpansberg—5	1952	Pine plantation
Zoutpansberg—6	1952	Pine plantation
Zoutpansberg—7	1952	Citrus plantation
Limpopo—2	1957	Rubbish dump in camp
D. opisthomelaina		
Nelspruit—4	1947	Subtropical fruit plantation
Mkuzi—2	1947	Game Reserve
Inhaca—6	1955	Domestic, on Island
Limpopo—3	1957	Rubbish dump in camp
D. séguyi		
Limpopo—4	1957	Rubbish dump in camp
Inhaca—7	1957	Forest, on Island

EYE PHENOTYPE AND HISTOLOGY

The macroscopic eye color phenotype of the four species of the melanogaster group is red in *D. melanogaster,* a slightly brighter red in *D. simulans,* and a still brighter red (nearly scarlet) in *D. opisthomelaina* and *D. séguyi.* In the last three species the various strains collected do not appear to show much variation from the normal phenotypes of the species, but in *D. melanogaster* some strain variation is evident. For example, the Zoutpansberg-3 strain has a slightly darker eye than the Zoutpansberg-4 strain, the Inhaca-1 strains has a more garnet-like eye than the other strains from this locality, and the eyes of the Stellenbosch-1 strain have a more brownish tone than the normal type.

The three species of the willistoni group have an eye color which is brighter than that of the foregoing species. In *D. willistoni* and *D. capricorni* it may be called orange red, while in *D. nebulosa* the color is even brighter.

All the wild type strains of *D. pseudoobscura* and *D. persimilis* are very similar in their eye color phenotype, this being a dull garnet red, while in *D. miranda* the color is somewhat darker. The eye colors of the mutants of *D. pseudoobscura* were as follows. In *v* and *or* the eye is bright red; in *pr* it is purplish brown; in *se* the colour is darker than in the previous mutant; in the combination *v se* the eye is yellow on emergence but darkens through brownish yellow to sepia; in *ca* the color is a dull red; in the combination *or pr* the eye is colorless; in *gl* the eye is a translucent yellow with fine red stipples. The three mutants of *D. persimilis* have the following eye colors. In *or* the color is bright red, but perhaps somewhat duller in tone than in the same mutant of the previous species. The mutant *cd* has a dull reddish garnet eye color which darkens to a duller tone with age. The mutant *ras* was received under the name of sepia, but is not allelic to the sepia of *D. pseudoobscura;* the color is

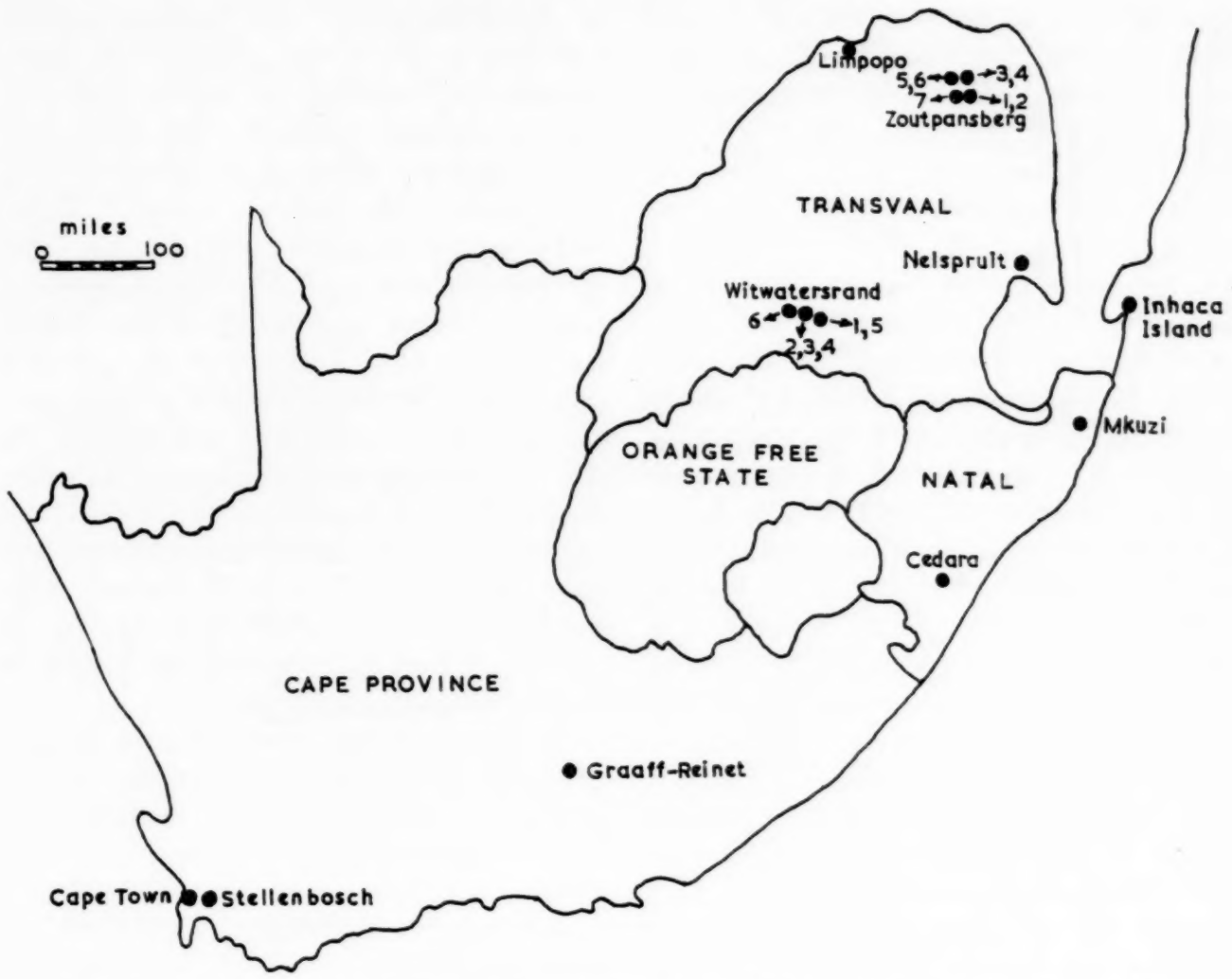

FIG. 1. The geographical distribution of the South African strains of the Drosophila species designated in table 1.

a darker sepia than that of the latter species.

In all essentials the histology of the compound eye of the other nine species is identical with that described for *D. melanogaster* and *Zaprionus vittiger* (Nolte, 1950). Exceptions noted were the following: the nuclei in the fenestrated zone of the eye of *D. capricorni* are located next to the layer of monopolars, instead of near the middle of the zone as in the other species, while in the species of the obscura group the post-retinal masses of pigment granules seem less continuous, being more stringlike in a radial direction. The mutant *gl* of *D. pseudoobscura* has a totally aberrant eye histology. The number of facets is reduced, the size of the individual facet is reduced and the shape is often distorted, or the facets are coalesced in pairs so that large spaces separate them. In these spaces hairs are found growing in clusters, sometimes up to seven in a group. The ommatidia are shorter but thicker than normal, and nuclei often seem to be distributed throughout the width of the secondary pigment cell region; in this region no pigment granules could be seen. Below the basement membrane large empty spaces often appear to separate the outer region of the eye from the innermost nerve tissue. The layer of monopolars as well as the external optic glomerulus are reduced in extent. Only the primary pigment cells seem to be more or less normal in appearance, the basal and post-retinal regions being absent.

In all the species the four pigment regions occur—primary, secondary, basal and post-retinal. For the species of the melanogaster and willistoni group the

gross color of sections of the eye is very similar to that described for *D. melanogaster* (Nolte, 1950), the primary pigment cells and the outer region of secondary cells having a salmon red color, whereas the remaining pigment regions are a purplish red. Slight differences are: the outer region appears to be more reddish in *D. opisthomelaina* and *D. willistoni* than in the other species; the post-retinal pigment masses in *D. capricorni* are more elongated radially, and separated to a greater extent than in the other species; the basal pigment masses in *D. capricorni* and *D. nebulosa* are smaller than in the other species. Of the species of the obscura group, *D. pseudoobscura* and *D. persimilis* have primary pigment cells with large brown granules, as was found by Cochrane (1936). The aggregate color of the other three regions is more reddish in hue than the purplish red of *D. melanogaster;* the basal pigment masses are smaller, and the pigment granules in the post-retinal region are separated into more discrete groups or masses than in the latter species, that is, they are seen to be contained in cells (cf. Cochrane, 1936). In *D. miranda* the primary cells contain a heavy concentration of brown granules, while the other regions are a darker red than in the other two species.

The mutants *v* and *or* of *D. pseudoobscura* have red granules only in all the pigment regions, excepting in the primary cells in which no pigmented granules are visible; the general impression of red is lighter than that of the wild type. The mutant *ca* is lighter red than the foregoing mutants but also with no pigmented granules in the primary cells; in the other regions the red color is due to granules which are reduced in number but increased in size, many granules having 2–4x the normal size. In the mutant *pr* the primary cells contain a heavy concentration of brown granules, while the aggregate color of the other pigment regions resembles that of the mutant brown of *D. melanogaster* but is more mauve purplish in hue; the granules in these regions are indistinct in outline as in the case of the latter mutant. The mutant *se* also resembles sepia of the latter species in general histological color (Nolte, 1954b), the primary cells having dark brown granules and the other pigment regions having smaller granules giving a general color impression of purplish wine; the post-retinal region is very narrow and the rhabdomeres are yellow. In the combination *v se* the aggregate color of the pigment regions is yellow, with no color in the primary cells. In the mutant *gl* only the primary cells contain pigmented granules which are brown in color and less in number, but larger in size, than in the wild type.

In *D. persimilis* the mutants *or* and *cd* resemble the bright red mutants of the previous species, the primary cells also being without pigmented granules. The mutant which has been named raspberry resembles the raspberry mutant of *D. melanogaster* (Nolte, 1950) in some respects. The primary cells are heavily pigmented with brown granules, while the remaining color is found in the secondary cells and is a reddish violet. The secondary pigment cells, or the granular masses thereof, seem to be more or less normal at the outer ends, but appear as stringlike masses throughout the main part of their length and then seem to peter out, often not reaching the basement membrane. The rhabdomes are yellow in color and around their bases groups of pigmented granules occur, each group being widely separated from the others. Post-retinal pigment masses are absent.

The Two Pigments

The red and brown pigments are present in the eyes of all ten species. The spectrophotometric curves of the two pigments, dissolved in AEA and AMA respectively, agree with those obtained for the wild type of *D. melanogaster* (Nolte, 1954a). In the brown pigment there is

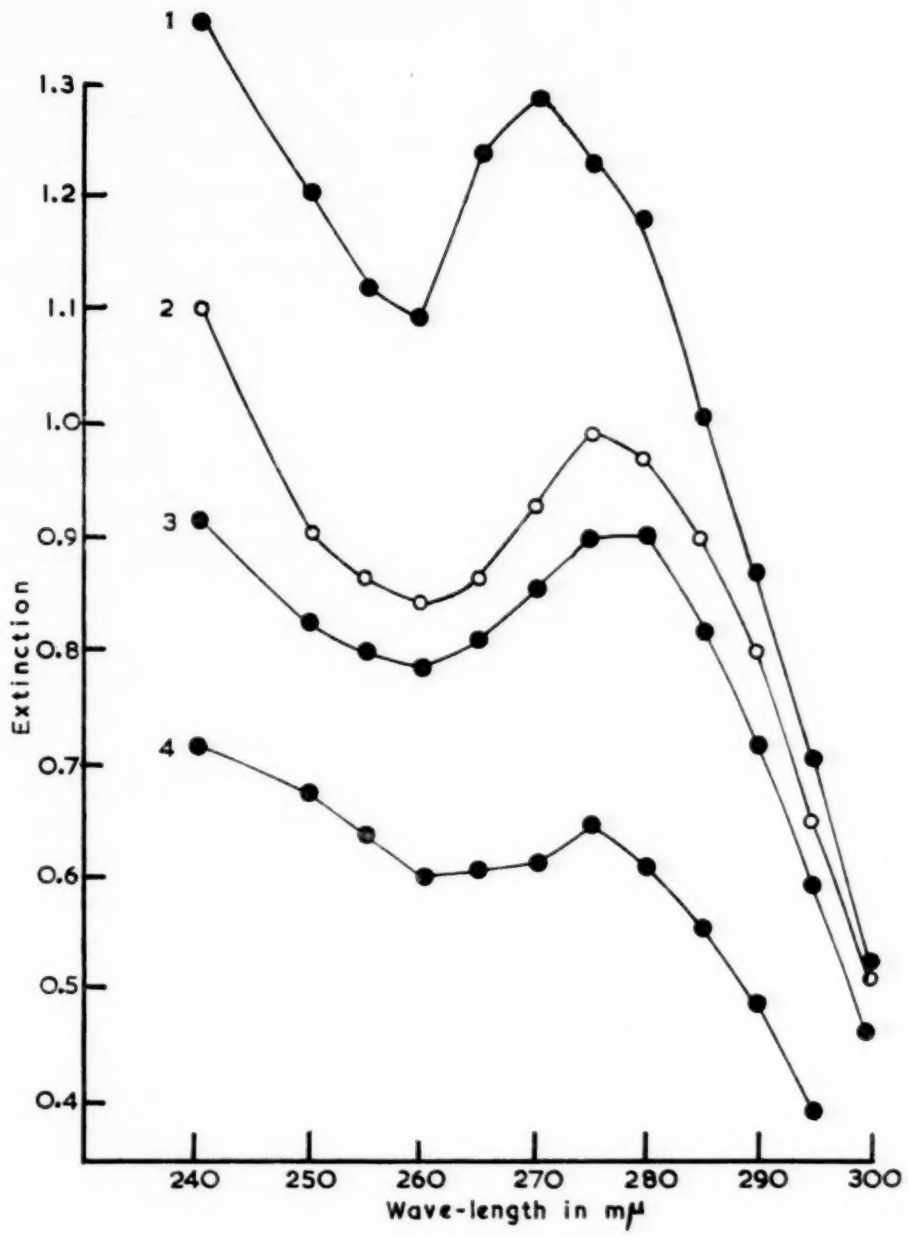

FIG. 2. Ultraviolet absorption curves of the red pigment extracted in AEA, for 10 heads per 1 cc. 1, *D. pseudoobscura,* the mutant sepia. 2, *D. melanogaster* wild type. 3, *D. pseudoobscura,* the Texas strain. 4, *D. pseudoobscura,* the Aspen strain.

a more or less continuous drop in light absorption in the ultra-violet and the visible spectrum, but with a slight peak at 444 mμ. For the red pigment of the species of the melanogaster and willistoni groups a valley occurs in the absorption at 260 mμ, followed by a sharp rise with a peak at about 280 mμ, then a sharp drop to the visible range, followed again by a sharp rise from about 400 mμ to form the bell-shaped curve with the peak of absorption at 480 mμ. However, for the various wild type and mutant strains of the three species of the obscura group, some variation occurs in the ultraviolet range. The valley and peak of absorption in this region seem somewhat flattened, for various strains, due to the low absorption varying between 255 and 260 mμ, and the high absorption varying between 275 and 280 mμ (fig. 2). In addition, the height between the valley and peak of absorption is less for these species than for the species of the melanogaster and willistoni groups. The curve for the red pigment of the Aspen strain of *D. pseudoobscura* appears to be atypical in the skewed peak it gives at 275 mμ.

The mutant *se* of *D. pseudoobscura* has a modified red pigment identical with that of the same mutant of *D. melano-*

TABLE 2. *Relative amounts of red and brown eye pigments of various strains of four species of the melanogaster group*

Strain	Red pigment	Brown pigment
D. melanogaster		
Canton—S	0.9162 ± 0.0109	0.0870 ± 0.0013
Oregon—R	0.9188 ± 0.0021	0.1043 ± 0.0036
Cape Town—1	1.0063 ± 0.0097	0.0991 ± 0.0038
Stellenbosch—1	0.5996 ± 0.0106	0.0858 ± 0.0012
Stellenbosch—2	0.9765 ± 0.0083	0.1137 ± 0.0016
Graaff-Reinet—1	0.9667 ± 0.0123	0.0966 ± 0.0017
Graaff-Reinet—2	1.1321 ± 0.0182	0.1227 ± 0.0022
Cedara—1	1.1070 ± 0.0225	0.1113 ± 0.0037
Cedara—2	1.0719 ± 0.0147	0.1268 ± 0.0026
Witwatersrand—1	1.0377 ± 0.0162	0.0950 ± 0.0012
Witwatersrand—2	1.0362 ± 0.0111	0.1050 ± 0.0016
Witwatersrand—3	0.9071 ± 0.0109	0.1098 ± 0.0017
Nelspruit—1	1.0982 ± 0.0073	0.1150 ± 0.0025
Nelspruit—2	1.0749 ± 0.0131	0.1112 ± 0.0018
Nelspruit—3	1.1062 ± 0.0166	0.1327 ± 0.0036
Inhaca—1	0.7107 ± 0.0162	0.1552 ± 0.0028
Inhaca—2	1.1577 ± 0.0128	0.1040 ± 0.0015
Inhaca—3	0.9014 ± 0.0090	0.1016 ± 0.0011
Inhaca—4	1.0656 ± 0.0144	0.1193 ± 0.0027
Inhaca—5	1.0550 ± 0.0173	0.0982 ± 0.0022
Zoutpansberg—1	1.0698 ± 0.0132	0.1026 ± 0.0038
Zoutpansberg—2	1.1034 ± 0.0101	0.1092 ± 0.0024
Zoutpansberg—3	0.9694 ± 0.0114	0.1253 ± 0.0018
Zoutpansberg—4	0.8768 ± 0.0074	0.0996 ± 0.0017
Limpopo—1	1.0637 ± 0.0076	0.1143 ± 0.0036
Mean of South African strains	1.0041 ± 0.0278	0.1110 ± 0.0031
F_1 Canton-S × Graaff-Reinet—2	0.9444 ± 0.0182	0.1102 ± 0.0070
Canton-S × Stellenbosch—1	0.8382 ± 0.0134	0.0838 ± 0.0023
D. simulans		
Stellenbosch—3	1.1163 ± 0.0460	0.1229 ± 0.0035
Witwatersrand—4	1.0705 ± 0.0096	0.1075 ± 0.0019
Witwatersrand—5	1.0139 ± 0.0095	0.1078 ± 0.0017
Witwatersrand—6	1.0708 ± 0.0315	0.1069 ± 0.0070
Mkuzi—1	1.0374 ± 0.0140	0.0968 ± 0.0031
Zoutpansberg—5	1.0614 ± 0.0207	0.1007 ± 0.0045
Zoutpansberg—6	1.0062 ± 0.0214	0.0938 ± 0.0021
Zoutpansberg—7	1.0531 ± 0.0081	0.1196 ± 0.0022
Limpopo—2	1.1250 ± 0.0176	0.1194 ± 0.0030
mean of South African strains	1.0616 ± 0.0143	0.1084 ± 0.0033
D. opisthomelaina		
Nelspruit—4	1.1128 ± 0.0237	0.1053 ± 0.0020
Mkuzi—2	1.1165 ± 0.0456	0.1174 ± 0.0050
Inhaca—6	1.1042 ± 0.0480	0.1038 ± 0.0028
Limpopo—3	1.1469 ± 0.0225	0.1230 ± 0.0027
Mean of South African strains	1.1201 ± 0.0083	0.1124 ± 0.0047
D. séguyi		
Limpopo—4	1.1352 ± 0.0095	0.1334 ± 0.0021
Inhaca—7	1.2036 ± 0.0076	0.1343 ± 0.0024
Mean of South African strains	1.1694 ± 0.0339	0.1339 ± 0.0005

gaster (Nolte, 1954b). The AEA solution has a greenish yellow color which becomes paler on standing and ultimately nearly colorless. In the ultraviolet the valley of absorption is at 260 mμ and the peak at 270 mμ, while in the visible region absorption drops, with, however, a small peak at 415 mμ. The mutant called raspberry of *D. persimilis* gives a normal absorption curve for the red pigment, that is, unlike the modified curve found for the raspberry mutant of *D. melanogaster* (Nolte, 1958a); however, the peak of absorption in the ultraviolet was much flattened.

PIGMENT QUANTITIES

The quantitative photometric estimations of the red and brown eye pigments in the three species groups are given in tables 2–4, the data being for extinction (E) and its standard error, at 480 mμ for the red pigment and at 444 mμ for the brown pigment, for concentrations of 10 heads per 1 cc. of the solvents AEA and AMA respectively. In each test 40 heads were extracted, and 10–12 experiments were made for each strain.

DISCUSSION

The differences in eye pigmentation between the ten species of *Drosophila* which were studied appear to be mainly of a quantitative nature for the red and brown pigments, differences being noted between groups, species and strains. However, some qualitative differences appear to exist.

(1) The brown pigment appears to be qualitatively identical in all the species.

TABLE 3. *The relative amounts of red and brown pigments in the eyes of the three species of the willistoni group*

Species	Strain	Red pigment	Brown pigment
D. willistoni	Idana	1.1436 ± 0.0152	0.1134 ± 0.0047
D. nebulosa	Belem	1.2988 ± 0.0348	0.1812 ± 0.0058
D. capricorni	Mogi	1.4824 ± 0.0246	0.2215 ± 0.0098

TABLE 4. *The relative amounts of red and brown eye pigments in the three species of the obscura group*

Strain	Red pigment	Brown pigment
D. miranda		
Big Bend	0.8138 ± 0.0226	0.2379 ± 0.0148
D. pseudoobscura		
Texas	0.8557 ± 0.0089	0.1940 ± 0.0050
Arrowhead, Aspen	0.6670 ± 0.0112	0.1877 ± 0.0081
Standard, Piñon Flats 340	0.8497 ± 0.0132	0.1766 ± 0.0024
Standard, Piñon Flats 345	0.7970 ± 0.0098	0.2023 ± 0.0050
Arrowhead, Piñon Flats 122	0.8234 ± 0.0059	0.1871 ± 0.0025
Arrowhead, Piñon Flats 126	0.9167 ± 0.0101	0.1843 ± 0.0035
Chiricahua, Piñon Flats 334	1.0425 ± 0.0185	0.2067 ± 0.0047
Chiricahua, Piñon Flats 352	0.9769 ± 0.0166	0.2039 ± 0.0062
Mean of Piñon Flats strains	0.9010 ± 0.0387	0.1935 ± 0.0050
vermilion (*v*)	0.7910 ± 0.0100	0.0049 ± 0.0004
orange (*or*)	0.9088 ± 0.0109	0.0053 ± 0.0005
claret (*ca*)	0.4439 ± 0.0097	0.0363 ± 0.0018
purple (*pr*)	0.0275	0.1714 ± 0.0030
sepia (*se*)	0.0549 ± 0.0019	0.2030 ± 0.0055
sepia at 415 mμ	0.2921 ± 0.0057	
vermilion sepia (*v se*)	0.0404 ± 0.0018	0.0133 ± 0.0008
vermilion sepia at 415 mμ	0.1753 ± 0.0123	
glass (*gl*)	0.0100	0.0114
D. persimilis		
Standard, Sequoia	0.9004 ± 0.0177	0.1667 ± 0.0028
Arrowhead, Porcupine Flat	0.9625 ± 0.0158	0.1902 ± 0.0035
orange (*or*)	0.8933 ± 0.0241	0.0053 ± 0.0008
cardinal (*cd*)	0.8826 ± 0.0130	0.0282 ± 0.0017
raspberry (*ras*)	0.1253 ± 0.0054	0.1738 ± 0.0053

The red pigment shows certain qualitative differences. Firstly, this pigment in the species of the obscura group appears to be more variable in its light absorption in the ultraviolet than in the other species. In these the valley of absorption is at 260 mμ and the peak at 280 mμ; for *D. miranda, D. pseudoobscura* and *D. persimilis* the lowest point of the valley varies from 255 mμ to 260 mμ, independently in various strains from the variation at the peak of from 275 to 280 mμ. For the pupae of *D. melanogaster* the valley has been found at 255 mμ and the peak at 280 mμ (Nolte, 1954a), so that qualitative changes do seem to occur in ultraviolet absorption by the red pigment. Secondly, the Aspen strain of *D. pseudoobscura* has been found to show a sharper, more skew, peak in the ultraviolet, i.e., a sharper rise in absorption from 270 mμ to 275 mμ than for the other strains of this species; it should also be noted that for the smaller quantity of red pigment in the eyes of this strain the peak should rather have been flattened.

(2) The quantitative comparison of the ten species must be based on relative sizes of the eye. A rough estimate has been made of the diameter of the eye, and in table 5 these estimates are given on a relative arbitrary scale. Whereas the species of the willistoni group have, totally and relative to body and eye size, larger amounts of both pigments than the species of the melanogaster group, the three species of the obscura group have a smaller amount of red pigment but a larger amount of brown pigment than the species of the other two groups. In table 5 are also given the ratios (R/B) between the amounts of red and brown pigment, computed from the data of tables 2–4. Generally for these ten species, the orderly decrease in the ratio is the result of three different factors. First, for species 1–4 the total amount of red pigment decreases in that order; secondly, for species 5–7 the increase in

TABLE 5. *The relative diameters of the eyes of the ten species, and the ratios between the amounts of red and brown pigments (R/B)*

	Species	Relative diameter of eye	R/B
1	*D. willistoni*	8	10.1
2	*D. opisthomelaina*	8¼	9.9
3	*D. simulans*	8½	9.8
4	*D. melanogaster*	8¾	9.0
5	*D. séguyi*	8¾+	8.7
6	*D. nebulosa*	9	7.2
7	*D. capricorni*	9½	6.7
8	*D. persimilis*	9	5.1–5.4
9	*D. pseudoobscura*	9	4.0–5.0
10	*D. miranda*	9½	3.4

brown pigment content is relatively greater, in that order, than the increase in red pigment content; thirdly, for species 8–10 there is a decrease in red and an increase in brown pigment content. The two pigments thus vary differentially in their content in these species.

Relative to eye size, the three more tropical species, i.e., the species of the willistoni group, have a higher total eye pigment content than the temperate to subtropical species of the melanogaster group, and these again have a higher total content than the three more temperate species of the obscura group. The three species groups can thus be differentiated on their eye pigment content. During the independent evolution of the melanogaster and willistoni groups from the obscura group (Patterson and Stone, 1952) the red pigment seems to have increased in both groups, but the brown pigment has decreased in the melanogaster group. The red pigment increase may partly be due to the deposition of red pigment also in the primary cells, this pigment being absent in these cells in the obscura group.

(3) Of the four South African species of the melanogaster group, the strains of *D. melanogaster* show a greater quantitative variation in eye pigment than the strains of the other three species. Among these strains a large number show significant deviations from the species mean. Of the 23 strains studied, at least 7 showed deviations in the red pigment content, 5 in the brown pigment content, and 4 in both pigments. Increase, or decrease in content of both pigments might be ascribed to differences in body size. Of the abovementioned strains, however, only the Graaff-Reinet-2 strain is appreciably larger in body, and eye size, than any other strain. The reasons for quantitative variation in eye pigment content in these various strains must, therefore, be sought for in genetic factors conditioning characteristics other than that of size. Although environmental factors, such as climate and food, in the various habitats of the strains may differ greatly, these could no longer have affected the quantitative data since most of the strains have been inbred under laboratory conditions for many years. The adaptation, genetically, of strains differing in this quantitative character, to different conditions of climate and habitat, has, however, to be considered.

In the first instance, it appears that general climatic factors do not play a part in the origination of differences in pigment content, since no significant trend is shown on comparing strains from the southwestern part of the country, which lies in the temperate winter rainfall region, with strains from the northeastern part, in the subtropical summer rainfall region. Secondly, although the habitats vary from a domestic environment in a temperate deciduous fruit region, to a subtropical fruit region, there is no consistent increase or decrease in one or both of the pigments in the strains from any particular locality. However, in nine out of thirteen strains from the hotter areas the amount of red pigment is greater than the mean for the species, although not significantly so in all cases.

On the other hand, inspection of the data of table 2 shows that variation between strains from one locality is often greater than the variation for the species; for example, the standard error for the red pigment content of the five Inhaca Island strains is ± 0.0787 as compared with the species standard error of ± 0.0278. In every single case in which two or more strains have been collected from a locality, significant differences occur in one or more of them in regard to one or both of the pigments. The fact that it is generally only one pigment which varies, proves that size differences are not implicated, and that such variation is genetic.

Some characteristics of this variation are the following: (i) The range of variation for both pigments is large; the red

pigment content ranges from 0.5996 to 1.1577, and the brown pigment content from 0.0858 to 0.1552. (ii) Often there is a differential quantitative effect on the two pigments. (iii) In certain cases, e.g., Nelspruit-1 and Nelspruit-2, which are derived from collections very close together, a population in one locality appears to have no quantitative variation. In other populations, e.g., Zoutpansberg-3 and -4, Graaf-Reinet-1 and -2, Inhaca-1 and -2, significant differences occur in both pigments, although each of these pairs of strains is derived from collections taken side-by-side. (iv) Quantitative differences are found in strains from collections taken during different years from a population of one particular locality, e.g., Nelspruit-2 and -3, Inhaca-3, -4 and -5, Witwatersrand-2 and -3. (v) The two American strains show a significant difference in their brown pigment content; in general, the South African strains have a higher content of both pigments than these two strains.

To test the type of genetic difference between strains several F_1 hybrids of crosses between Canton-S and wild type South African strains were tested for eye pigments. The results in table 2 show that in the hybrids of crosses between strains intermediate amounts of both pigments are found.

In a previous study (Nolte, 1958b), in connection with the heterozygous effect of eye-color genes, the question was put as to whether many of the different wild type eye-color genes do not exist in multiple allelic series. Arising from the data of that investigation, it also appeared, however, that modifying genes of a different type are active in affecting the final quantitative results of the eye pigmentary processes. In one wild type strain these genes appeared to be of a dominant nature as regards the red pigment but of a recessive nature as regards the brown pigment, in comparison with a second strain. A survey of the quantitative data of the present investigation favors the second possibility rather than the first. It appears as if two series of polygenes are segregating in most wild populations of *D. melanogaster,* and they affect the total content of red and brown pigments respectively. The fluctuations found in a particular population from year to year would merely depend on the genotypes of the sample collected.

(4) Strain differences in eye pigment content also occur in both *D. pseudoobscura* and *D. persimilis,* the most striking being in the chromosomal types of the former species. In the Piñon Flats collection of strains from neighbouring areas, the two Standard strains show significant differences in the amounts of both pigments, while in the Arrowhead and Chiricahua pairs of strains the differences lie only in the red pigment. On the other hand the Chiricahua strains have higher amounts of both pigments than the three Arrowhead strains studied. It is postulated that in this species, as in the South African strains of *D. melanogaster,* two series of polygenes, affecting the total content of red and brown pigments respectively, are segregating in wild populations.

It is interesting to speculate on the possible interrelationships of these genes with the gene arrangements of the chromosomal types, Standard, Arrowhead and Chiricahua. That these types have adaptive values has been demonstrated in various ways, the following being some of the findings for the populations of Piñon Flats. Dobzhansky (1943) found the Standard arrangement most frequent in winter and early spring, the Chiricahua type most frequent in early summer, and the Arrowhead type showing the least change in frequency. In population cage work Dobzhansky (1948) found Standard homozygotes, at 25° C, much superior in fitness to Arrowhead homozygotes, and the latter much superior to Chiricahua homozygotes. The relative adaptive values of Standard and Chiricahua homozygotes, and their heterozy-

TABLE 6. *The amounts of the two pigments in the eyes of various mutants, expressed as percentages of the amounts found in wild type strains*

Species	Mutant strain	% Red pigment	% Brown pigment
D. pseudoobscura	*v*	87	2.5
	or	101	2.8
	ca	49	18
	pr		89
	se	6	105
D. persimilis	*or*	96	3
	cd	95	16
	ras	13	98
D. melanogaster	*v*	95	5.2
	cn	96	5
	ca	27	29
	p	40	33
	bw		97
	se	6	142
	cd	108	15
	ras²	15	103
	ras	25	110

gotes, were found to depend on the microorganisms used in the food of the flies and the larvae (da Cunha, 1951). Spassky (1951) found Chiricahua homozygotes showing higher viability at high temperatures and in dry food, while Arrowhead homozygotes show higher viability at cooler temperatures and in humid media. In the collections tested for eye pigment the Chiricahua type does seem to possess more of the postulated effective polygenes conditioning increased eye pigment than does the Arrowhead type.

(5) Gene homologies between different species of *Drosophila* have been worked out or postulated (Sturtevant and Tan, 1937; Sturtevant and Novitski, 1941; Spencer, 1945; Patterson and Stone, 1952). Due to absence of hybridization and to the fact that the mode of biochemical action of most eye color genes is unknown, it is somewhat difficult to precisely homologize some of these mutant genes. However, to supplement the evidence of known loci for these genes in some particular chromosome, the various secondary properties of mutant eyes may be compared for two species, as well as the amounts of the two pigments, expressed as percentages of the normal amounts in the wild strains of each species. In table 6 some calculations of the latter type are given for the species *D. pseudoobscura* and *D. persimilis* as compared with *D. melanogaster,* the figures for the latter species being taken from previous investigations (Nolte, 1952, 1954a, 1954b, 1955). The mutants *v* of *D. pseudoobscura* and *D. melanogaster* are homologous, judging by the results of eye transplantation work (Gottschewski and Tan, 1938), by their localization in the X chromosome, and by their percentages of pigments in table 6; in both species this mutant is somewhat smaller in size than the wild type. According to the same criteria the mutants *or* of *D. pseudoobscura* and *D. persimilis* are homologous with *cn* of *D. melanogaster;* the loci of *or* in chromosome 3 and *cn* in chromosome 2R agree well with the presumed chromosome homology. The mutant *pr* of *D. pseudoobscura* certainly seems equivalent to *bw* of *D. melanogaster* when judged on the distances of their loci from *or* and *cn* respectively; the histological picture of pigmentation in the eyes of these two mutants is identical, and so also is the percentage of brown pigment compared with the wild type of the two species. The mutant *se* of these two species is also identical if judged on their loci, the presence of the yellow modification of the red pigment, and the percentage of this pigment as compared with the red pigment of the wild type, and also the fact that the brown pigment content is higher than in the wild type. The mutant *ca* of *D. pseudoobscura* is homologous with *ca* of *D. melanogaster* if judged on the localization of these genes in chromosomes 2 and 3R respectively, and on the decrease in number but increase in size of the pigment granules. This particular strain of mutant of *D. pseudoobscura* could equally well be ho-

mologous with the chromosome 3 mutant *p* of *D. melanogaster* which also has a reduced number but increased size of granules and which is more nearly equivalent in regard to the percentage of red pigment; this *ca* differs from both mutants in the latter species in having no pigmented granules visible in the primary pigment cells.

The locus of the mutant of *D. persimilis* received as *cd* could not be determined in chromosome 2; the percentages of the two pigments, however, correspond to those of the mutant *cd* of *D. melanogaster,* a mutant located in chromosome 3R. The strain received as *se* has been renamed raspberry (*ras*) because of its properties: it is sexlinked, the pigment cells are disarranged, and the percentages of pigments compare well with those of the raspberry mutants of *D. melanogaster* —it is primarily a structural gene and not a pigment gene, as in the latter species (Nolte, 1952). The mutant *gl* of *D. pseudoobscura* is also a structural gene.

These data on the comparison of eye color mutants of *D. pseudoobscura, D. persimilis* and *D. melanogaster* indicate that in *Drosophila* species the eye color genes are homologous, whether conditioning eye structure or the production of pigments, but that the pigmentary process as a whole has become modified in various groups and species during the course of the evolutionary sequences. Any such gene mutating will, however, produce a mutant with very similar effects in different species genotypes.

Summary

A comparative study was made of the compound eye and its pigments in four South African species of the melanogaster group of the Sophophora (*D. melanogaster, D. simulans, D. opisthomelaina, D. séguyi*), three Brazilian species of the willistoni group (*D. willistoni, D. nebulosa, D. capricorni*), and three North American species of the obscura group (*D. pseudoobscura, D. persimilis, D. miranda*). The following were the most important findings.

(1) The histology of the eye is very similar in all ten species, there being four pigment regions—primary, secondary, basal and post-retinal—with granules containing red and brown pigments. The species of the obscura group differ from the other groups in that brown pigment only occurs in the primary pigment cells. During the evolution of the melanogaster and willistoni groups from the obscura group the process of eye pigmentation was apparently modified by the addition of red pigment deposition in the primary cells.

(2) Spectrophotometric analysis of differential extracts of eyes in AEA and AMA show that the eyes of all ten species possess the same two pigments, a red and a brown. The spectrophotometric curve of the red pigment of the species of the obscura group shows slight deviations from that of the other two groups, specifically in the ultraviolet absorption.

(3) Quantitative photometric estimations of the red and brown pigments show that the three species of the willistoni group, relative to eye size, have a higher total pigment content than the four species of the melanogaster group. The three species of the obscura group have, totally and relative to body and eye size, a smaller amount of red pigment but a larger amount of brown pigment than the species of the other two groups. During the evolution of the latter groups the red pigment content has increased, perhaps due to deposition in the primary as well as the other pigment cells, but in the melanogaster group the brown pigment content has decreased.

(4) Of the four South African species, wild type strains of *D. melanogaster* show a greater quantitative variation than wild type strains of the other species. This variation occurs in either the red or the brown or in both pigments. Generally this variation cannot be ascribed to size

differences, nor to differences in the natural habitats of the strains, but must be based on genetic differences. This genetic variation indicates the presence of two series of polygenes independently affecting the amounts of red and brown pigment, and these polygenes seem to be segregating in most of the populations studied.

(5) Strain differences in eye pigment content also occur in wild type strains of *D. pseudoobscura*. Various Standard, Arrowhead and Chiricahua chromosomal type strains show significant differences in the amounts of one or both of the pigments. It is postulated that in this species also two series of polygenes affecting the total amounts of red and brown pigments respectively are segregating in wild populations.

(6) Evidence is used, from the histology of the eye pigment regions and the percentages of red and brown pigments in mutants as compared with the wild type, to demonstrate the homology of various eye color genes in *D. pseudoobscura, D. persimilis* and *D. melanogaster*. These genes have apparently exactly similar expressions in the three species, although the eye pigmentary system as a whole has become slightly modified during evolution.

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THE AVERAGE EFFECT OF RADIATION-INDUCED MUTATIONS ON VIABILITY IN *DROSOPHILA MELANOGASTER*[1]

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INTRODUCTION

A number of basic postulates of population genetics appear so nearly self-evident that they are generally accepted with a minimum of experimental proof. Outstanding in this respect is that of the unfavorable effect of most mutations on viability. Geneticists assume that a vast majority of mutations are detrimental. This assumption rests chiefly on observations on strains of various experimental organisms containing various major mutants and on the consideration that "normal" organisms are products of a long continued natural selection. It is indeed true that most mutations that are useful in genetic experiments (in fact, most mutations easily detectable by the geneticist) have marked deleterious effects on the viability or fertility of individuals; one need only glance through Bridges and Brehme's *"The Mutants of Drosophila melanogaster"* (1944) to find numerous examples of such effects. It is also true that the so-called "wild-type" individuals of any species represent the culmination of a long evolutionary process and that the genes established in the gene pool of a Mendelian population have been exposed to many generations of selection. It is reasonable to suppose, then, that the gene components of any gene pool are those with the greatest likelihood of producing individuals that are well adapted to the prevailing environment.

It does not follow from what has been said above that an overwhelming majority of gene mutations are harmful. This conclusion would follow only if one assumes that the constellation of genes selected for within the gene pool of a population consists of one and only one wild-type allele at each locus. For selection to achieve this result, the adaptive values of heterozygous individuals must always be intermediate with respect to—at any rate, not superior to the better of—the two corresponding homozygotes. Under these conditions selection tends to produce populations of homozygous individuals. Should this be the case, it does indeed follow that virtually all newly mutated genes should be harmful to their carriers both in the homozygous and heterozygous condition. Under these circumstances gene mutation is a process which acts contrary to natural selection and which burdens each population with a load of harmful genes. The size of this load is determined by mutation rates and by the efficiency of selection (see, for instance, Muller, 1950).

The assumption that selection necessarily tends to produce a homogeneous population in which every individual carries identical sets of genes is an essential element in the above argument. And yet, it is usually admitted that a population of this sort would be fit only for an environment of a constancy which never exists in fact. In order to cope with the inconstancy of any real environment a population must possess some genetic and some phenotypic heterogeneity. This heterogeneity may be even more necessary for those species characterized by a high degree of behavioral complexity—of which man is the extreme case—where some of the most important components

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of fitness involve interactions between individuals. In a constantly shifting environment selection is probably not consistent in choosing or rejecting alternative alleles at a large number of loci. The challenge of an environmental shift may often be most rapidly and effectively met by heterozygous rather than homozygous individuals and this will have the effect of continuing genetic heterogeneity. As a result of the complex ramifications of gene interactions—for instance rapid secondary selection for genetic modifiers in the heterozygous condition—it may develop that the most favored individuals at any given time will, in reality, be complex heterozygotes. Finally, even within a constant environment, heterozygous individuals may have, simply as a result of their heterozygosity, adaptive values superior to those of homozygotes (the superiority of heterozygosity *per se* is an important part of the thesis Lerner sets forth in his book, *"Genetic Homostasis"* (1954)).

It is apparent, then, that there are reasons not only for suspecting that selection within a Mendelian population is not outstandingly successful in producing populations of homozygous individuals but also for believing that in reality selection does not tend to produce homozygosity in most populations. If the selection for uniform populations results from homozygote superiority, it is convenient to regard the selection for genetic diversity in terms of heterozygote superiority. The extreme form taken by this model would be a gene pool consisting of a large series of unique alleles at each locus. Every individual in this type of population would be completely heterozygous. Since no homozygous individuals could, by definition, be present in such a population, the behavior of the different alleles when homozygous would have no bearing on selection for their retention in or elimination from the gene pool.

It is impossible, of course, to maintain a gene pool consisting solely of unique alleles. If such a pool existed at any time, the Poisson distribution predicts that in the following generation nearly 37% of the alleles at any locus would be lost from the population, only 37% would remain unique, while 18%, 6%, and 2% of the alleles at each locus would be present two, three, and four or more times respectively. This type of chance elimination and duplication of alleles cannot be forestalled. The existing situation within any Mendelian population, consequently, must lie somewhere between complete homozygosis and complete heterozygosis. Two fundamental problems of population genetics, then, can be stated as follows: First, to establish the extent to which populations deviate from the completely homogeneous genetic structure postulated on the basis of the absolute selective superiority of homozygous individuals. Second, to determine the underlying causes for this deviation. The mere enumeration of known instances of heterozygote superiority or of genetic diversity between individuals, although useful for certain purposes, is an inadequate approach to these problems. Well-documented instances of balanced polymorphism are of necessity available only for those cases in which heterozygotes differ markedly from each of the corresponding homozygotes. Therefore, it is hardly conceivable that the number of well-analyzed cases will ever exceed more than a small percentage of the number of loci postulated for Drosophila or for any other higher organism. On the other hand, it is also possible that these obvious cases of heterozygote superiority are only a small proportion of the total number of instances in which heterozygotes actually do possess a selective advantage. Until information is available that indicates the latter possibility has some basis in fact, it will be arguable that polymorphic systems based on heterosis or heterozygote superiority are relatively rare situations of no great importance to the genetics of

populations. The experiments reported here represent an attempt to approach these problems through a study of the effects of new mutations in heterozygous condition on the viability of otherwise homozygous individuals. The results of these experiments have been reported previously in a preliminary report (Wallace, 1957).

The Argument

The two extreme models of the genetic structure of populations, based respectively on homozygote and heterozygote superiority, can be represented as shown in figure 1. Under each model it is possible to illustrate (1) genotypes representative of the outcome attained by selection under ideal conditions, the "ideal" genotypes, (2) genotypes representing individuals as they might actually exist in a population, "normal" genotypes, (3) genotypes of individuals made homozygous by special breeding techniques, and (4) genotypes similar to those of (3) with the exception that new genetic changes have been induced at random in one of the two otherwise identical chromosomes. The figure, like the experimental procedures to be described later, is limited to illustrating a single chromosome.

The ideal genotype under selection for homozygosis in a constant environment is, by definition, completely homozygous; genetically, all individuals in a population of this sort would be identical. On the contrary, the extreme selection for heterozygosity would lead to an array of ideal genotypes in which every gene locus is occupied by two different alleles as shown in the figure. Furthermore, if the formation of homozygotes within a population is to be avoided, each allele at every locus would have to differ from every other allele; under these circumstances no two individuals would have similar alleles at any locus. This situation has been represented in the figure by the use of subscripts.

The genotypes of normal individuals of an actual population must fall short of the theoretical, ideal situation. In the case of homozygote superiority, certain loci would be occupied by mutant alleles not yet eliminated by natural selection. These might represent mutations of relatively recent origin or alleles which were useful at some earlier time but which, as a result of a change in the direction of selection, are now in the process of replacement by other alleles. In general, the relative frequency of these mutant alleles among all loci is considered small (Muller, 1956). In the case of "new" recessive mutations, their frequencies can be calculated from mutation rates and selective disadvantages; semi-dominance would cause these genes to have frequencies even lower than those calculated on the basis of complete recessivity.

In the case of heterozygote superiority, normal genotypes would fall short of the ideal for two reasons, homozygosis and ill-adapted heterozygotes. Despite any amount of selection, certain alleles will be represented several times within a population and, consequently, individuals homozygous for these alleles will be formed occasionally. Furthermore, alleles which have an average deleterious effect even in the heterozygous condition will arise by mutation and will persist in low frequency in the population.

Homozygosis for entire chromosomes with their hundreds or thousands of genes is an entirely artificial situation made possible only by the use of special genetic techniques. It is well known from studies with Drosophila that individuals homozygous for chromosomes obtained from large populations have lower viabilities than individuals heterozygous for random pairs of these same chromosomes. This is true even if one excludes from the experimental material chromosomes—such as lethals and semi-lethals—with obvious drastic negative effects on the viability of homozygotes. The low viabilities of homozygous individuals is predicted by

both models. Under homozygote superiority, deleterious mutations exist in a population as the result of mutation pressure and because of recent changes in the direction of selection. Consequently, when many loci are made homozygous simultaneously as when individuals are made homozygous for an entire chromosome, there is an excellent chance that one or more of these deleterious genes will become homozygous and, hence, that the viability of the homozygous individual will be impaired. It is important to note, however, that the relative proportion of loci occupied by these deleterious genes is small, according to this model, and that for the vast majority of loci the genotype of any homozygote is identical to or better than that of a normal individual heterozygous for a random pair of chromosomes. Under heterozygote superiority the situation is quite different although the immediate consequences appear the same. Here the poor viability of the homozygotes can be ascribed to homozygosis for alleles which have been retained in the population on the basis of their behavior in heterozygotes. By definition the viability of heterozygotes is on the average the highest attainable; the alleles retained to form these heterozygotes may be lethal, semilethal, or subvital when homozygous. However, under this model the genotype of the artificially produced homozygote differs markedly from that of the ordinary individual of the population; the normal genotype has been pictured as one heterozygous for genes at many if not at nearly all loci while the homozygote is homozygous for one or another of these alleles at every locus of the experimentally controlled chromosome.

The contrast in the degree to which individuals homozygous for chromosomes taken from a population differ genetically from individuals commonly found within the same population leads to different predictions concerning the viability effects on homozygous individuals of new mutations present in one but not in the other of these otherwise identical chromosomes. Under homozygote superiority we have seen that the genotypes of homozygous individuals are essentially the same as the one postulated as ideal with the important exception that one or more loci are occupied by deleterious mutations. If one were to irradiate one of the chromosomes for which these individuals are homozygous, one would induce a small amount of heterozygosity in this series of homozygous loci. By far the most probable change would consist of the mutation of a "normal" gene to a deleterious form and, hence, the viability of the "homozygote" would be lowered still more. Neglecting epistatic interactions, an improvement in viability would result only by the coincidence of two rare events; first, the mutation of a deleterious gene and, second, the change of this gene to a more normal allele. The fact that mutant alleles with minute deleterious effects (viability of homozygous individuals between .999 and 1.000) may not occupy a negligible fraction of all loci of a chromosome obtained from a large population does not alter the above expectations. Presumably, the more minute the effect of the original allele on viability, the smaller the chance that a random change will lead to something better. One expects, then, that only a negligible proportion of these new mutations will be "beneficial" to the viability of homozygous individuals.

The model based on heterozygote superiority leads to quite different expectations. First, the artificially created homozygote is homozygous for alleles at many loci at which heterozygosity was described as the normal condition; a mutation at any of these loci must, by definition, lead to heterozygosity. Furthermore, it was explicit in the extreme model that there are many alleles at every locus capable of participating in selectively advantageous heterozygous combinations; consequently, a random mutation must

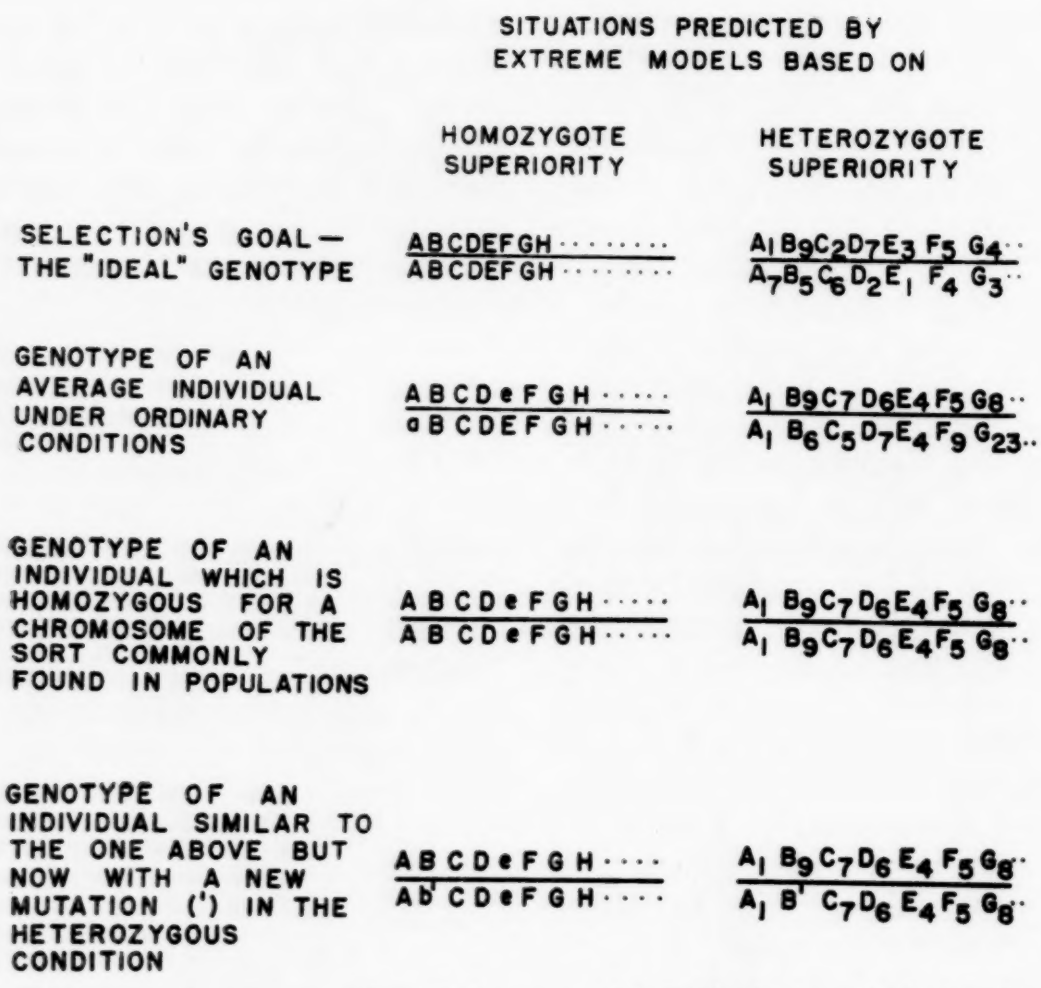
SITUATIONS PREDICTED BY EXTREME MODELS BASED ON
HOMOZYGOTE SUPERIORITY
HETEROZYGOTE SUPERIORITY
SELECTION'S GOAL — THE "IDEAL" GENOTYPE
ABCDEFGH·····
ABCDEFGH·····
A1 B9C2D7E3 F5 G4··
A7B5C6D2E1 F4 G3··
GENOTYPE OF AN AVERAGE INDIVIDUAL UNDER ORDINARY CONDITIONS
A B C D e F G H·····
a B C D E F G H·····
A1 B9C7 D6E4 F5 G8··
A1 B6C5 D7E4 F9 G23··
GENOTYPE OF AN INDIVIDUAL WHICH IS HOMOZYGOUS FOR A CHROMOSOME OF THE SORT COMMONLY FOUND IN POPULATIONS
A B C D e F G H·····
A B C D e F G H·····
A1 B9C7 D6E4 F5 G8··
A1 B9C7 D6E4F5 G8··
GENOTYPE OF AN INDIVIDUAL SIMILAR TO THE ONE ABOVE BUT NOW WITH A NEW MUTATION (') IN THE HETEROZYGOUS CONDITION
A B C D e F G H····
Ab' C D e F G H····
A1 B9 C7 D6 E4 F5 G8··
A1 B' C7 D6 E4 F5 G8··

FIG. 1. Diagrammatic representation of the types of individuals, hypothetical and otherwise, expected in populations under two extreme models of genetic structure. An experimental method for distinguishing between the two models is explained in the text.

have a finite chance of producing one of these alleles. Therefore, new mutations should with some measurable frequency improve the viability of homozygotes when such mutations are present in the heterozygous condition. This point needs further amplification. It is not necessary under the model of heterozygote superiority that every new mutation improve the viability of the "homozygous" individuals. This has been indicated in the figure and earlier in the discussion; the genotype illustrated in figure 1 has been shown to differ from the "ideal" genotype by possessing an allele (G_{23}) which we define as one which has an average deleterious effect on viability even when heterozygous. It is, of course, impossible to predict how frequent such alleles are among the entire array of allelic forms at a given locus. Furthermore, the model based on heterozygote superiority does not predict that a random array of new mutations will, on the average, improve the viability of homozygous individuals. Should the average effect of new mutations be deleterious, the actual proportion of "heterotic" mutations can be estimated by an analysis of means and variances by a technique analogous to one described by Wallace and Madden (1953). Should the proportion of heterotic mutations calculated by this technique be found to be relatively low (less than 20%, for example), the final judgment as to the validity of the model based on heterozygote superiority would have to be based on allelism tests and the distribution of heterotic mutations among all loci. The occurrence of a low frequency of heterotic changes at many loci would be consistent with the model; the occurrence of a high frequency of heterotic mutations at a relatively small proportion of all loci would

not. In the latter case, the gene pool could be considered as being made of two parts; in one, the genetic structure would resemble that of the model based on homozygote superiority; in the other, that of the alternative model.

Material and Methods

Source of material. The material used in this study consisted of four quasi-normal chromosomes obtained from our experimental population #18. This is a population that had been in our laboratory for approximately 310 weeks prior to these experiments; for the first 210 weeks of this time it was known as population #5. Population #5 was started during April 1950 with a number of non-lethal, non-semilethal second chromosomes obtained from an Ore-R stock maintained in mass culture at Cold Spring Harbor. Chromosomes other than the second in this population were of mixed origin, part were from the Ore-R stock, others were from the CyL/Pm stock used in the manipulation of chromosomes in genetic tests. (Cy, L, and Pm refer to the dominant second chromosome genes Curly wing, Lobe eye, and Plum eye; the CyL chromosome has two inversions which prevent recombination between it and chromosomes of the standard gene sequence.) For 210 weeks population #5, a small population of about 1000 adults, was exposed continuously to 5r per hour of gamma-radiation. At the end of this period a large egg sample (several food cups with approximately 10,000 eggs each) was removed from #5 and was placed in a new population cage, #18. This population was allowed to expand in size to about 10,000 adults which is normal for our cages. This population, #18, was not irradiated.

During the 100 weeks that population #18 was maintained in the absence of radiation it was subjected to periodic genetic tests (Wallace, 1956). These tests consisted of analyzing second chromosomes for their effect on the viabilities of flies carrying them in the homozygous condition or, using the same chromosomes, in random heterozygous pairs. The most striking change in this population following the cessation of irradiation was a decrease in the frequency of lethal chromosomes. Specifically, there was a loss of one particular lethal whose high frequency in population #5 led to a corresponding high frequency of chance allelism of lethals among the random heterozygotes of that population.

The chromosomes chosen for the experiments described below were obtained from one of these routine tests of population #18 (our sample #174). The experimental technique described below precludes the use of a "random" choice of chromosomes as our starting material; it was necessary to choose chromosomes which, when homozygous, produced viable and fertile flies. From sample 174 four test cultures yielding homozygous wild-type flies were chosen from among 36 cultures of this type. The identification numbers (cage-sample-assistant-chromosome number) and the results of these routine tests are listed in table 1. The fertility of the homozygous wild-type flies was verified in subsequent tests.

Preliminary preparation. The preliminary preparation of this material consisted of transferring each of the four chromosomes into the genetic background of our CyL/Pm stock. This was accomplished (fig. 2) by repeated backcrosses of single CyL/+ males to CyL/Pm females. The material obtained from sample 18-174 had already undergone two such backcrosses; these were continued for at least an additional 9 generations. Each individual ex-

Table 1. *Numbers (n) and relative proportions (r.v.) of flies of the four genotypes in the homozygous test cultures from which the chromosomes for the present study were obtained.* The identification number of the test cultures lists population—sample number—assistant—chromosome.

Test culture		CyL/Pm	CyL/+	Pm/+	+/+	Total
18–174–III–11	n	53	45	46	45	189
	r.v.	1.00	0.83	0.85	0.83	—
18–174–III–13	n	96	100	87	91	374
	r.v.	1.00	1.03	0.90	0.94	—
18–174–III–14	n	66	57	64	73	260
	r.v.	1.00	0.85	0.96	1.09	—
18–174–III–18	n	85	92	92	71	340
	r.v.	1.00	1.07	1.07	0.83	—

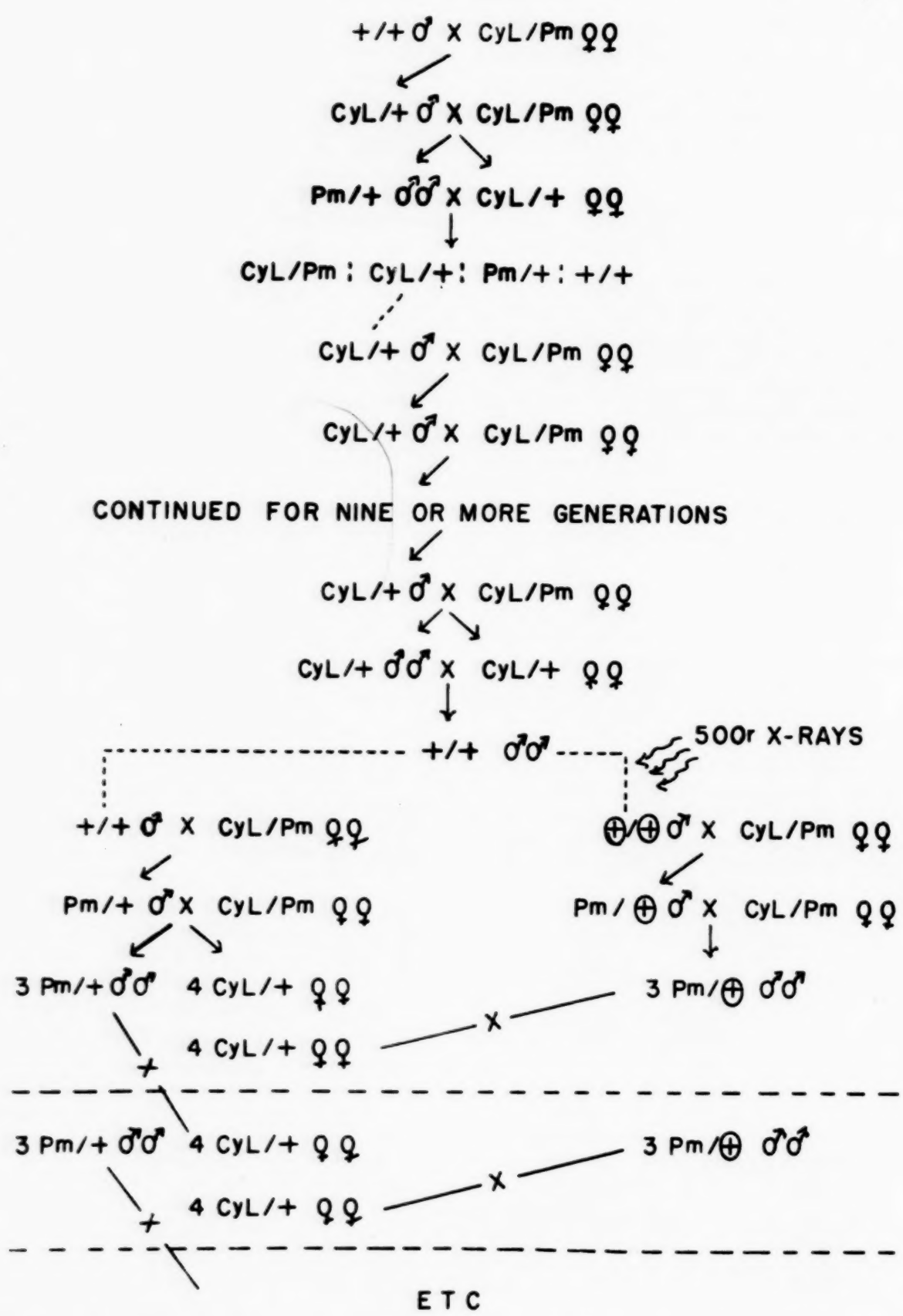

FIG. 2. An outline of the source and preparation of material and of the method used for studying the viability effects of mutations in heterozygous condition.

periment consisted of testing only one of these four chromosomes, so meanwhile the other three stocks were kept by continuing the backcrosses of single CyL/+ males with CyL/Pm females. By the end of the time covered by this report, 20 generations of such crosses had elapsed.

It is important to note the use of a single Cy/+ male in each backcross generation. This restriction prevented the accumulation of a variety of second chromosomes in each line. While it is true that the chromosome (for example, 18-174-III-11) tested in one experiment could differ somewhat from the supposedly same

chromosome tested in a subsequent one, nevertheless, within any one experiment second-chromosome variation was kept at a minimum.

General technique. The crux of these experiments lies in the comparison of the relative viabilities of flies homozygous for one or another of the four chromosomes described above and of flies homozygous for the same chromosome but heterozygous for new genetic changes induced by X-irradiation in one member of the chromosome pair. The experimental procedure is outlined in figure 2. From a backcross culture approximately 50 CyL/+ males and females were obtained. These flies, brothers and sisters, were mated in some 12 culture bottles and from these cultures about 400 wild-type males were collected. These males were homozygous for the particular second chromosome carried by the CyL/+ male of the backcross culture. For convenience, the homozygous wild-type flies are designated as the parental (P) generation.

The 400 males were divided into two lots of equal size, one of which was x-rayed. As a rule these males were four days old or less at the time of treatment. The exposure consisted of 500r given at a rate of 100r per minute for five minutes. Details of the treatments were as follows: 140 Kv, 6 ma, target distance 9½", 0.85 mm Aluminum filter, Norelco X-ray machine. Following irradiation the x-rayed and control males were stored in fresh vials for two days.

The choice of 500r was governed by two considerations: First, the genetic model under investigation is not concerned with the effects on viability of gross chromosomal aberrations. Second, it was desirable to include in the irradiated material as many mutations as possible, otherwise the irradiated series would in large part be identical with the control. It appeared that 500r was a level of irradiation likely to produce a considerable number of mutations with a minimum number of gross chromosomal aberrations.

The procedures following irradiation were altered occasionally during the course of the experiments; the following represents a general account of the technique used while a discussion of specific changes will be postponed until later. The X-ray ((+)/(+)) and control (+/+) males were mated individually with CyL/Pm females in vials. Single Pm/+ or Pm/(+) F_1 males were obtained from each of these cultures and these males were again mated singly with CyL/Pm females. From each control culture, three Pm/+ F_2 males and eight CyL/+ F_2 virgin females were obtained; as they were collected, these flies were stored in three vials, the males in one and four of the females in each of the other two. From each of the X-ray cultures, 3 Pm/(+) F_2 males were obtained and these, too, were stored in vials.

The F_3 cultures were the final test cultures of each experiment. For the X-ray series, the parents of each culture consisted of the Pm/(+) F_2 males of one X-ray culture and four of the CyL/+ F_2 females of a control culture. For the control series of F_3 cultures the parents consisted of Pm/+ F_2 males of one control culture and the CyL/+ F_2 females of a *different* control culture. Brother-sister matings were avoided in the control series of cultures in order to insure the same relationship between parental males and females in both the X-ray and control cultures. The number of F_3 cultures for each series varied from 50 to 100 from experiment to experiment.

The offspring expected in the F_3 cultures were of four types:

Control—CyL/Pm : CyL/+ : Pm/+ : +/+

X-ray—CyL/Pm : CyL/(+) : Pm/+ : +/(+)

In each series these four classes are expected to occur with equal frequencies. The number of parents, however, was sufficiently large to cause overcrowding of larvae and under these conditions expected Mendelian ratios become distorted as the result of differential viabilities and developmental rates. The CyL/Pm flies which, as a result of the preliminary backcrosses, had X, 3rd, and 4th chromosomes typical of the CyL/Pm stock, were chosen as the standard by which to measure the viability of flies of the other three classes. If the viability of the CyL/Pm flies is considered to be 1.000, an unbiased estimate of the relative viabilities of the CyL/+, Pm/+, and +/+ flies is obtained by dividing the number of flies in these three classes by one more than the number of CyL/Pm flies (Haldane, 1956). These ratios were obtained for each culture and the estimates of the relative viabilities of the three classes in each of the two series, control and X-ray, were obtained by averaging the ratios of individual cultures.

The above calculations yield information concerning the relative viabilities of CyL/Pm (1.000 by definition), CyL/+, Pm/+, and +/+ flies in each of the two series. Now, if we assume that the CyL/Pm flies in the two series are comparable, the results of these same calculations allow us to compare the relative viabilities of flies of the same genotypes between the two series; that is, CyL/+ of the control with CyL/(+) of the X-ray series, Pm/+ of the control with Pm/+ of the X-ray, and +/+ of the control with +/(+) of the X-ray. There are a number of reasons for believing that this comparison is a valid one. First, neither the CyL nor the Pm chromosome of the CyL/Pm flies of either series has been irradiated. Sec-

ond, the genetic background of these CyL/Pm flies in each series is that found in the CyL/Pm stock. Third, although the irradiation has undoubtedly induced genetic changes in the third and fourth chromosomes of the X-ray series (the irradiated X-chromosomes are lost in the first mating), these have been "diluted" by two post-irradiation crosses with CyL/Pm females. Fourth, in addition to being "diluted" these irradiated chromosomes (other than the second) are distributed at random among the four classes of flies in the F_3 X-ray cultures (with the exception of 2-3 or 2-4 translocations which would always be found in the CyL/(+) and +/(+) but *not* in the CyL/Pm nor Pm/+ flies). Besides these four reasons for believing the comparison to be a legitimate one, there are empirical checks the most obvious of which is a comparison of the relative viabilities of the Pm/+ flies of the two series. In neither the X-ray nor the control series do these flies carry irradiated non-Plum chromosomes; hence, if the CyL/Pm flies of the two series are indeed equal, the Pm/+ flies of the two series should also have the same relative viabilities.

Specific changes in experimental techniques. During the course of these experiments specific aspects of the experimental procedure have been changed from time to time. These changes, which differ from the preceding generalized account, and which occasionally deal with additional points, are itemized below.

1. Distribution of X-ray and control cultures among assistants. Through a misunderstanding, the control and X-ray cultures of the first experiment were counted by different persons. Since it was impossible to ascribe differences between the two series to the irradiation rather than to personal differences, this experiment was discarded. This report deals with experiments #2–#9 in which virtually equal numbers of control and X-ray F_3 cultures were counted by each person.

2. Coding of bottles. The X-ray and control F_3 cultures of experiments 2 and 3 were labeled as such. In the fourth and subsequent experiments, the F_3 matings were made by one person and the bottles of the two series were intermingled and numbered consecutively according to a code prepared for each experiment from a table of random figures. Under this coding scheme, one (either the first or the second) of every consecutive pair of cultures was X-ray while the other was control; the relative position of the two bottles of each pair was randomized.

3. Temperature. Ostensibly, these experiments were carried out at 25°. However, the constant temperature room is relatively large and has a temperature gradient from floor to ceiling. Since each assistant uses a different tier of shelves, this means that there is a temperature gradient "between persons." Ordinarily this gradient is not great but during one period of exceptionally cold weather the temperature in the constant temperature room dropped so that the lower shelves were at approximately 22°. In correcting this situation, the circulation of air in this room was improved and the mean temperature was raised to 26°. Since Curly wings tend to become straight at low temperature, especially in the last counts of over-crowded cultures, tests for systematic misclassification of flies were made in the F_3 cultures that were hatching during the cold period and, later in a subsequent experiment. These tests will be described in another section.

4. Numbers of parents. The number of female parents in the F_3 cultures was changed during the experiments. In experiment #2, 3 CyL/+ females were used per culture; in all subsequent experiments four females were used as described above.

5. Identification of experiments. In experiments #2–#5 final cultures were set up in two lots separated by a week's time and these lots were identified as 2A, 2B, 3A, 3B, etc. Since a direct comparison of control and X-ray data is possible only within lot A or lot B, each of these (2A, for instance) has been considered a separate experiment. Consequently, this study consists of twelve experiments with three experiments being devoted to each of the four chromosomes.

6. Mating scheme. The outline of the mating scheme given in figure 2 does not apply to experiments 2 and 3. In these early experiments, Pm/(+) males and Pm/+ males and CyL/+ females were obtained directly from the first mating (wild-type males with CyL/Pm females). There were two reasons for changing the procedure to the more lengthy one shown in the figure. First, in the abbreviated technique, each of the three Pm/(+) males of the irradiated series carried a different irradiated chromosome. This would affect the calculation of "between-culture" variances in this series and, perhaps, preclude a direct comparison of these variances with those of the control series (all sources of variability other than that of the newly induced changes are the same in the two series of cultures). Furthermore, there is evidence (see, for instance, Lewontin, 1955) that cultures containing a variety of genotypes support larger numbers of individuals than do cultures in which the developing individuals are similar. There was an undesirable possibility, then, that the X-ray cultures containing three different irradiated chromosomes would yield higher numbers of wild-type flies than the control simply because there were three different types of wild flies

developing in these cultures. This possibility had to be avoided. Finally, it seemed desirable to add an additional generation in the mating procedure in order to "dilute" irradiated background chromosomes and decrease the importance of possible interactions between these third and fourth chromosomes and the CyL and Pm chromosomes of our standard class of flies.

There was a valid reason for choosing the original, shorter mating scheme; namely, to minimize selection in the choice of experimental material. Obviously, the irradiated chromosomes capable of being tested are those free of dominant lethals and other dominant or semi-dominant factors with severe effects on viability. Lengthening the mating procedure by an additional generation does give selection a greater opportunity to remove these grossly deleterious mutations from our material. Data are available which indicates that this is not an important factor: in a series of 331 matings of Pm/(+) F_2 males, 10 failed to leave offspring; in a similar series of 324 matings of Pm/+ F_2 males of the control series, 4 failed to leave offspring.

7. Counting the F_3 cultures. The F_3 cultures were usually counted three times—on the 10th day after mating, the 13th or 14th day, and the 17th or 18th day. In experiment 7 an attempt was made to have these cultures counted four times (10th, 12th or 13th, 14th or 15th, and 17th or 18th day after mating). It was impossible to schedule counts of this sort conveniently, however, so this method of counting was abandoned.

Additional remarks concerning techniques. A few remarks concerning the nature of the genetic technique used in these experiments should be made in this section. One assumes in calculating the relative viabilities of the four classes of flies from the numbers which hatch in each test culture that the developing larvae do not influence one another in any way, that is, that there are no inter-larval interactions. If this were true, the removal of one class of larvae would not alter the relative viabilities of the remaining three classes. Surprisingly enough, this is a remarkably accurate description of the actual situation. In a quite different series of tests of chromosomes taken from different experimental populations and tested in homozygous (relatively few wild-type flies per test culture, many cultures with none at all) and heterozygous (many, usually more than the expected 25%, wild-type flies per culture) condition, the average ratio of CyL/+ to CyL/Pm in each of the two series was 1.07 to 1.00. The relative viability of CyL/Pm flies in these cultures as in the present experiments was 1.00 by definition. In the case of Pm/+ flies, however, the corresponding ratios were 1.11 and 1.15 to 1.00 in homozygous and heterozygous cultures respectively. This difference which is undoubtedly significant can be ascribed almost exclusively to Pm/lethal heterozygotes; flies of this type hatch in greater relative proportions in cultures within which many wild-type flies are developing. Obviously, then, there are interactions among developing larvae. In the current experiments, though, the frequency of induced lethals among the irradiated chromosomes is not expected to exceed 2%–3%; it seems unlikely that these lethals are frequent enough or that the larval interactions are large enough to interfere seriously with the interpretation of the experimental data.

Finally, mention should be made of a failure to randomize the culture bottles in setting up the F_3 cultures. This is important in connection with an analysis of variance that will be discussed later. When culture bottles are prepared, they are stored at 16° in baskets that hold 30 bottles each. All bottles in one basket are generally prepared at the same time; bottles in different baskets, however, may have been prepared at different times, a difference of several days perhaps. In setting up the F_3 cultures, it was the practice to proceed in order I-X-ray, I-control, II-X-ray, etc. where I, II, III, and IV refer to different assistants; the bottles for these matings were simply taken from one basket after another. Since the baskets during this time were piled in a haphazard order as far as elapsed time since preparation was concerned, bottles of different ages were probably distributed at random between the X-ray and control series and between different assistants. However, within an experiment, the bottles in one basket were too numerous to be depleted, say, by the X-ray cultures of one person and, consequently, the remaining bottles would be used in the control bottles of that same person. A basket of bottles not depleted in the control series for one person would, however, be used for the X-ray cultures of the succeeding person. This distribution of similar bottles between the control cultures of one person and the X-ray cultures of another may bias the results of the analysis of variance towards interactions involving assistant and treatment.

Experimental Results

A summary of the observed ratios of CyL/+ and CyL/(+), Pm/+, and +/+ and +/(+) flies to CyL/Pm flies is given in table 2. The data are presented in terms of the mean ratios observed by each of four persons (I–IV) in each of the 12 experiments; the numbers of cultures upon which these means

TABLE 2. *A summary of the average relative viabilities of flies of different genotypes observed by each of four persons in twelve experiments.* The relative viability of CyL/Pm is 1.000 by definition. n = number of cultures on which the average is based.

	Control				X-ray			
Exp.-Asst.	CyL/+	Pm/+	+/+	n	CyL/⊕	Pm/+	+/⊕	n
2A–I	1.047	1.119	1.033	12	1.086	1.096	1.091	13
II	1.086	1.212	1.062	13	1.082	1.258	1.105	13
III	1.103	1.117	1.065	12	1.106	1.142	1.078	12
IV	1.063	1.183	1.055	12	1.093	1.110	1.062	12
2B–I	1.077	1.187	.979	15	1.043	1.143	1.011	15
II	1.159	1.293	1.149	15	1.196	1.329	1.157	15
III	1.133	1.137	1.075	15	1.175	1.182	1.131	15
IV	1.146	1.107	1.071	15	1.101	1.117	1.057	15
3A–I	1.043	1.028	.974	13	1.110	1.119	.976	12
II	1.122	1.150	.920	13	1.157	1.153	.991	12
III	1.055	1.066	.995	12	1.120	1.046	.947	11
IV	1.021	1.023	.912	12	1.068	1.091	.959	12
3B–I	1.023	1.071	.922	13	.975	.962	.870	13
II	1.028	1.134	.962	13	1.165	1.208	1.079	13
III	1.023	1.102	.917	10	1.103	1.069	.952	12
IV	1.135	1.185	.999	12	1.005	1.073	.991	11
4A–I	1.102	1.102	.903	13	1.113	1.141	.970	13
II	1.085	1.229	1.017	13	1.141	1.182	.982	13
III	1.233	1.338	1.147	12	1.115	1.120	1.062	12
IV	1.069	1.184	1.033	12	1.108	1.171	1.033	12
4B–I	1.074	1.071	.913	12	1.163	1.113	.988	12
II	1.142	1.241	.985	12	1.063	1.126	1.006	12
III	1.043	1.080	.931	13	1.095	1.095	.995	13
IV	1.014	1.008	.931	13	1.079	1.086	1.031	13
5A–I	1.147	1.222	1.152	13	1.113	1.164	1.192	13
II	.986	1.108	1.021	13	1.114	1.165	1.128	13
III	1.088	1.148	1.007	12	1.157	1.113	1.035	12
IV	1.101	1.150	1.077	12	1.086	1.059	.970	12
5B–I	1.163	1.227	1.076	12	1.193	1.115	1.074	12
II	1.180	1.347	1.191	12	1.030	1.175	1.068	12
III	1.060	1.169	1.032	13	1.022	1.072	.913	13
IV	1.092	1.155	.990	13	1.082	1.155	1.030	13
6–I	1.039	1.012	.957	25	1.051	1.106	1.003	25
II	1.164	1.222	1.062	25	1.143	1.241	1.123	25
III	1.191	1.142	1.070	25	1.196	1.153	1.119	25
IV	1.106	1.203	.906	25	1.204	1.247	1.096	25
7–I	.979	1.044	.872	25	1.095	1.057	.937	25
II	1.008	1.175	1.007	24	1.034	1.062	.915	24
III	1.074	1.043	.897	25	1.156	1.084	.984	25
IV	1.036	1.125	.988	25	1.094	1.116	1.036	25
8–I	1.086	1.155	.993	20	1.127	1.070	.992	20
II	1.167	1.228	1.019	20	1.161	1.234	1.044	20
III	1.243	1.176	1.055	20	1.205	1.206	1.080	20
IV	1.125	1.211	1.011	20	1.157	1.181	1.083	20
9–I	1.089	1.044	1.051	20	1.133	1.094	1.058	20
II	1.093	1.195	1.121	20	1.121	1.187	1.099	20
III	1.114	1.081	.964	20	1.105	1.087	.982	20
IV	1.110	1.199	1.059	20	1.114	1.162	1.030	20
Weighted avg.	1.094	1.146	1.008	766	1.115	1.137	1.033	764

are based are also listed in the table. The outstanding feature of the table is the weighted average which indicates that the CyL/(+) and +/(+) flies of the X-ray series have somewhat higher ratios than the corresponding classes of the control series. The ratios of Pm/+ flies in the two series are quite similar, as expected.

If one tabulates the relative sizes (control minus X-ray) of these ratios for the individual entries of table 2, one finds (table 3) that the similarity of the Pm/+ flies extends to this type of analysis (control ratios exceeded those of the X-ray series in 23 comparisons of 47). The ratios of CyL/(+) and +/(+) flies of the X-ray series exceeded those of the control in two-thirds or more of the individual comparisons.

Taken at face value these data offer strong evidence in favor of the model of population structure based on heterozygote superiority. An increase in the *mean* viability is so unexpected, however, that a careful and extended analysis of the data and of the experimental assumptions is absolutely necessary. One wonders, for instance, about the apparent increase of mean viability brought about by heterozygosity for "random" mutations; the argument, it will be recalled, did not rely on an increase of the mean but merely on the detection of a fairly high frequency of heterotic mutations. Second, one wonders about the magnitude of the apparent heterotic effect. Had the irradiated chromosomes been tested in the homozygous condition, an exposure to 500r might be expected to induce detectable viability mutations in some 20% of them; if only part of these genetic changes give rise to new heterotic combinations, the heterosis in individual instances must be quite pronounced. Finally, one wonders about the viability of CyL/(+) flies which appears higher than the CyL/+ individuals of the control series. These CyL/(+) flies are heterozygous for second chromosomes derived from two different strains; the

TABLE 3. *Number of times the average relative viabilities of the control cultures exceed or are less than those of the X-ray cultures as indicated in table 2.*

Genotype	Control exceeds X-ray	X-ray exceeds control	No test	Total
CyL/+	16	32	0	48
Pm/+	23	24	1	48
+/+	14	33	1	48

argument presented in the preceding section did not predict that random mutations would increase the viability of heterozygous individuals, even of heterozygous individuals with rather poor viabilities.

The remainder of this paper deals with a variety of analyses of the data upon which table 2 is based and with experimental tests of certain factors which might possibly bias the result in the observed direction.

Comparison of observed relative viabilities by t-test. The most direct test of the significance of the data listed in table 2 is that of the differences between X-ray and control series observed by each person in each of the 12 experiments. The mean difference (control − X-ray) in the case of Pm/+ flies, $\bar{d}$, is + .0148, $s_{\bar{d}} =$ .0100, $t = 1.48$, $p = .15$. This difference is not significant. In the case of CyL/+ and CyL/(+) flies, $\bar{d} = -.0185$, $s_{\bar{d}} =$ .0089, $t = 2.09$, $p = .04$. For +/+ and +/(+) flies, $\bar{d} = -.0206$, $s_{\bar{d}} = .0090$, $t = 2.29$, and $p = .02$. The larger relative viabilities of the CyL/(+) and +/(+) flies of the X-ray series appear to be significant. (The discrepancies between the differences of this test and those shown in the last entry of table 2 arise because the latter are weighted means while the t-test described here is based on unweighted differences.)

Analysis of variance of observed ratios. Assuming that the observed ratios were valid measures of viability, variance analyses were made to compare different sources of error and to determine the significance of the observed results. Since

there were *a priori* reasons for expecting the different classes of flies to behave differently with respect to irradiation, each class has been analyzed separately. (It was expected that the Pm/+ flies of the two series would not differ and it seemed doubtful whether the CyL/+ and +/(+) flies would react in the same way to the newly induced mutations.)

The analysis is capable of revealing differences between treatments (control versus X-ray), between persons (including both real differences in the environmental conditions under which their material is handled and differences resulting from different work habits), between the four original chromosomes, between replicated experiments using the same chromosomes, as well as the first- and second-order interactions of these main sources of error.

The results of the analyses are given in table 4. Irradiation has had no detectable effect on the Plum flies. The differences between the Curly Lobe flies and the wild-type flies of the X-ray and control series are significant at the 5% and 1% levels, respectively. The analyses show, too, that each of the remaining primary causes of variation has had a detectable effect. The variation between assistants is due in part at least to the temperature gradient mentioned earlier but to some extent must accompany consistent differences in work habits. Significant differences between chromosomes simply reflect the choice of four different chromosomes as our initial material; no two chromosomes obtained from a population need be the same.

Leaving the primary sources of error, the outstanding feature of the analysis is the general lack of significance for first- and second-order interactions. None of the interactions involving treatment is significant; in the case of treatment-chromosome interaction this means that all four chromosomes reacted similarly to the presence of new mutations. The exceptional instances of assistant-chromosome and assistant-experiment interactions do not influence the interpretation of the significant effect accompanying irradiation; it seems most likely that these interactions are caused by the non-random distribution of cultures mentioned in the discussion of techniques.

There is no doubt, then, that the differences in relative ratios of flies listed in table 2 are significant in the case of Curly Lobe and wild-type but not in the case of Plum flies.

Numbers of flies. As a first test of the meaningfulness of the comparison be-

TABLE 4. *Summaries of the results of analyses of variance of culture size and of the relative viabilities of the three types of flies—CyL, Pm, and wild-type.* m.s. = mean square, F = F-ratio, p = probability that the observed F-ratio has occurred by chance.

Sources of error	d.f.	Culture size			CyL/+			Pm/+			+/+		
		m.s.	F	p	m.s.	F	p	m.s.	F	p	m.s.	F	p
Main effects:													
Treatment	1	2.7	—	—	.1781	5.88	<5%	.0335	1.01	—	.2479	7.40	<1%
Assistant	3	19499.7	5.68	<1%	.1604	5.29	<1%	.7647	23.10	<1%	.2071	6.18	<1%
Chromosome	3	316582.6	92.14	<1%	.2972	9.81	<1%	.4929	14.89	<1%	.8620	25.73	<1%
Exp. in chr.	8	165046.2	48.04	<1%	.0773	2.55	<1%	.0845	2.55	1%	.0524	1.56	—
1st order interactions:													
Treat.-asst.	3	2956.1	—	—	.0057	—	—	.0041	—	—	.0154	—	—
Treat.-chr.	3	1621.9	—	—	.0386	1.27	—	.0576	1.74	—	.0687	2.05	—
Treat.-exp. in chr.	8	9995.1	2.91	<1%	.0218	—	—	.0401	1.21	—	.0298	—	—
Asst.-chr.	9	6023.3	1.75	—	.0819	2.70	<1%	.0451	1.36	—	.1768	5.28	<1%
Asst.-exp. in chr.	24	7382.8	2.15	<1%	.0393	1.30	—	.0602	1.82	1%	.0396	1.18	—
2nd order interactions:													
Treat.-asst.-chr.	9	3328.0	—	—	.0189	—	—	.0070	—	—	.0096	—	—
Treat.-asst.-exp. in chr.	24	4312.1	1.26	—	.0324	1.07	—	.0445	1.34	—	.0368	1.10	—
Error	1434	3435.9	*	*	.0303	*	*	.0331	*	*	.0335	*	*

tween ratios of flies, one may consider the numbers of flies hatching per culture in each of the two series. It would be unreasonable, for instance, to adhere rigidly to conclusions based on comparisons of ratios if, by virtue of large differences in the numbers of flies hatching per culture, it seemed that growth conditions in the two series were vastly different.

The mean number of flies per culture in the 766 control cultures was 375.81 while the corresponding number for the 764 cultures of the X-ray series was 375.90. The difference between means is less than 0.1 fly!

The results of an analysis of variance of total flies per culture has been listed in table 4 along with the analysis of relative viabilities. Irradiation, as we have just seen, has had no effect on the mean numbers of flies yielded per culture. In addition to the significance of the other primary sources of error (assistants, chromosomes, experiments within chromosome) there are a number of significant interactions. This variation can be ascribed to differences in the age of culture media in bottles at the time F_3 matings were made and to the non-random distribution of these bottles *within experiments* among the X-ray cultures of one person and control cultures of another. To indicate the magnitude of differences which appear highly significant by this test, the mean numbers of flies per culture in bottles counted by different persons may be cited—367.65, 373.36, 377.66 and 384.58.

Comparison of X-ray and control variances. The error variances shown for the four analyses listed in table 4 represent the averages of the combined error variances of the X-ray and control series in each instance. An indication of the array of culture sizes or of observed ratios of the three different classes of flies can be obtained from a comparison of the error variances of X-ray and control series computed separately; the pertinent data are listed in table 5. (Error variance is the variance between individual cultures counted by one person in one experiment averaged through all persons and all experiments.)

The data shown in table 5 indicate that, as one might expect, the variation among the ratios of CyL/(+) and +/(+) flies of the X-ray series is larger than among the corresponding classes of flies for the control series; only the CyL/(+) class shows a significant difference, however. The variances among the ratios of Pm/+ flies of the two series are nearly identical. In the case of total flies per culture, the variance of the X-ray series is slightly, but no significantly, less than that of the control series.

The similarity of both means and variances of the total numbers of flies per culture in the two series, control and X-ray, indicates that the culture conditions under which the flies of the two series developed were indeed similar. This similarity lends substantial support towards acceptance of the implications of the data listed in table 2.

Information regarding the frequency distributions of cultures of different sizes and of the relative viabilities of various classes of flies is summarized in table 6 and figure 3. The pertinent aspects of these data are (1) the similarity of the distributions of numbers of flies in the control and X-ray series which indicates that irradiation has not destroyed the basis for comparing the two series, (2) the similarity of the distributions of the relative viabilities of Pm/+ flies in the two series of cultures which is a reflection of the similarity of the CyL/Pm flies, the standard class, in the two series, and

TABLE 5. *Summary of the error variances for numbers of flies per culture and of relative viabilities of flies of the three genotypes computed separately for control and X-ray cultures*

	Control	X-ray	F	p
Culture size	3780.50	3290.86	1.09	—
CyL/+	.028317	.032270	1.14	5%–1%
Pm/+	.033191	.033069	1.00	—
+/+	.032185	.034864	1.08	—

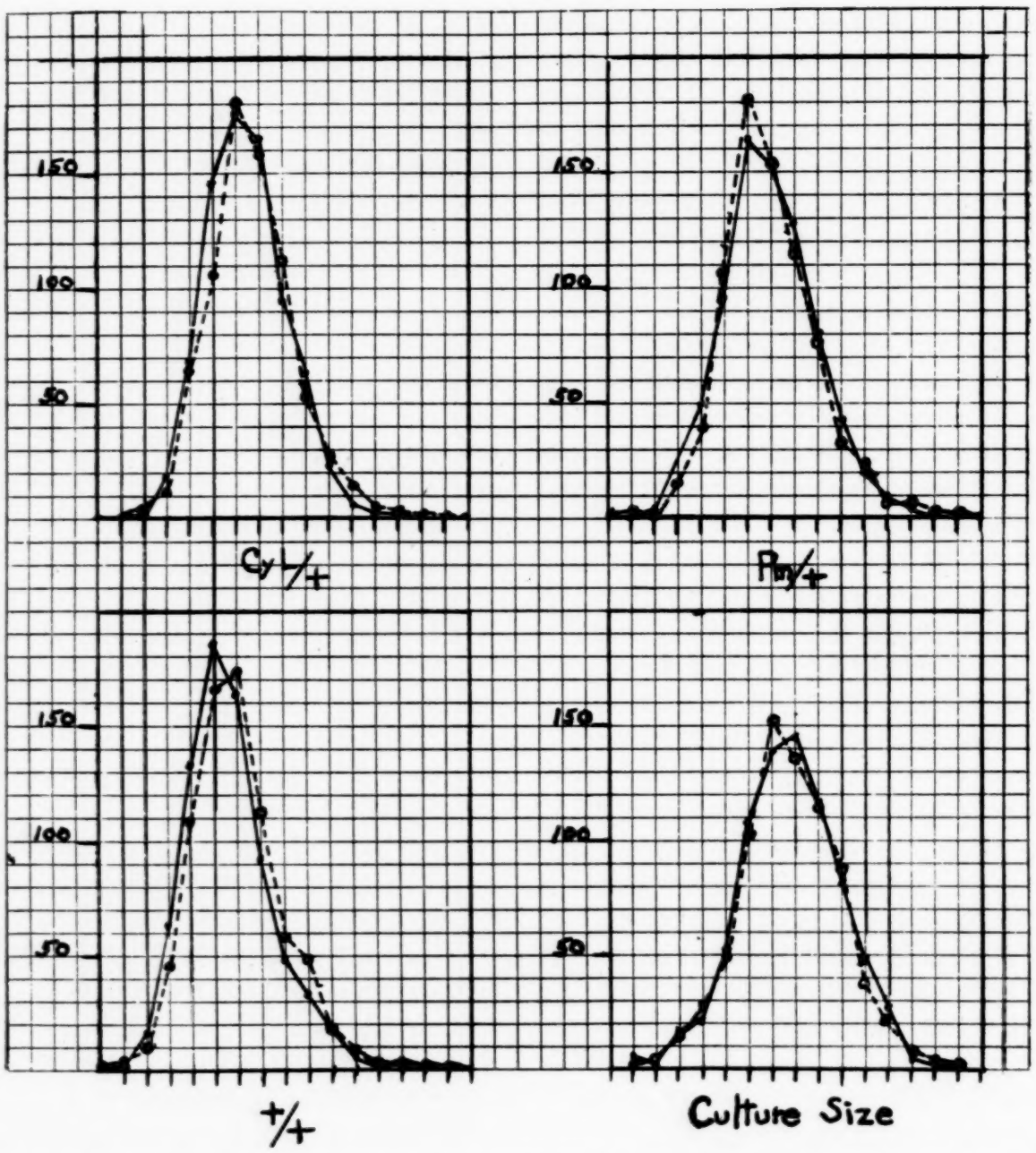

FIG. 3. Frequency distributions of culture sizes and of relative viabilities of flies of different genotypes in control and X-ray series. Y-axis = number of cultures; X-axis = culture size on relative viability as indicated in table 6. Solid line, control; dotted line, X-ray.

(3) the upward shift in the viability of wild flies of the X-ray series which embraces the entire distribution curve and not simply an isolated portion of it.

Analysis of ratios and numbers of flies in successive counts. One of the more disturbing possibilities raised by the data listed in table 2 is that the higher ratio of "heterozygous" wild flies in the X-ray series represents a greater mortality of CyL/Pm flies in that series rather than a greater viability of wild-type flies. An indication that this is not the case is given by the equality of the Pm/+ flies of the two series, an equality expected on the grounds of genetic similarity and seemingly verified by the data. Nevertheless, if the mortality-viability relationships within the cultures were rather complex, the ratios of Pm/+ flies could conceivably achieve equality as the result of a series of compensating accidents. Further insight can be obtained on this point by examining the numbers and ratios of flies of different genotypes at different times during the existence of the F_3 cultures. If some of the individuals of the three classes of flies carrying mutant

TABLE 6. *Frequency distributions of culture sizes and of relative viabilities of CyL, Pm, and wild flies in control and X-ray cultures.* n = number of flies per culture, r.v. = relative viability (CyL/Pm = 1.000), c = control cultures, x = X-ray cultures.

				CyL/+		Pm/+		+/+	
n	c	x	r.v.	c	x	c	x	c	x
<166	4	2	<.49	0	0	0	0	1	0
167–199	1	2	.50	0	0	0	1	3	1
200–232	16	14	.60	0	2	3	0	16	10
233–266	21	28	.70	19	12	14	16	63	46
267–299	53	50	.80	69	66	50	38	131	119
300–332	109	104	.90	146	113	95	116	185	167
333–366	139	154	1.00	176	180	164	182	163	173
367–399	145	135	1.10	165	158	153	152	92	111
400–432	116	114	1.20	95	126	128	115	49	58
433–466	81	87	1.30	64	54	80	76	34	48
467–499	48	39	1.40	22	28	43	32	19	18
500–532	27	23	1.50	6	15	21	22	5	7
533–566	4	8	1.60	2	6	10	6	1	2
567–599	1	3	1.70	1	2	4	6	3	1
600+	1	1	1.80	0	1	0	1	0	0
			1.90	0	1	1	1	1	2
			2.00+	1	0	0	0	0	1
Total	766	764		766	764	766	764	766	764

genes died as a result of interactions between these genes (Cy, L, and Pm) and mutations induced on the third and fourth chromosomes by irradiation, one would expect to find somewhat smaller numbers of flies in the early counts of the X-ray cultures with the deficiency resulting primarily from low numbers of mutant flies. Since the total number of larvae developing in a culture bottle exceeds the number which that culture can support, an early numerical deficiency need not necessarily persist and be observed in the total counts described above.

Four experiments covering the four different chromosomes were chosen for analysis—3A and 3B (treated in this instance as one experiment), 6, 8, and 9. Experiments 3A and 3B were substituted in this analysis for #7, because four counts rather than three had been made of the flies in the F_3 cultures of the latter experiment. The analysis consists of comparing the ratios and number of Curly Lobe, Plum and wild-type flies to CyL/Pm in the first count, in the first and second counts combined, and in the three counts. The latter is, of course, the contribution of these four experiments to the data listed in table 2 and discussed above.

The results of these analyses are listed in table 7. There is no indication in these data that during the time the early larvae are developing there is a higher mortality of flies in the X-ray than in the control bottles. In the first count there are actually more flies of every genotype in the bottles of the X-ray series than in those of the control. In the second count the total numbers have become quite similar but still the numbers of flies of all genotypes except CyL/Pm are greater in the X-ray than in the control cultures. Finally, as we have seen above, the total counts of cultures of both series are very similar and, therefore, the numbers of flies of the different genotypes approach the calculated relative viabilities.

An examination of ratios in the early counts shows (table 7) that the relative proportion of wild-type flies in the X-ray series is higher than that of the wild-type flies in the control series; this is so

TABLE 7. *Analysis of the numbers of flies and the relative viabilities of flies of each genotype observed in the first, first two, and all three counts of control and X-ray cultures.* These data include experiments 3A, 3B, 6, 8, and 9 only. r.v.* = relative viability based on the average number of flies shown in the table. r.v. = relative viability for the same cultures based on the mean of the relative viabilities calculated for each culture separately.

Count	Control						X-ray					
	No.	CyL/Pm	CyL/+	Pm/+	+/+	Total	No.	CyL/Pm	CyL/⊕	Pm/+	+/⊕	Total
1st	354**	11985	14350	13920	10717	50972	352*	12566	15043	14488	11748	53845
	Avg.	33.86	40.54	39.32	30.27	143.99	Avg.	35.70	42.74	41.16	33.38	152.97
	r.v.*	1.000	1.197	1.161	.894	—	r.v.*	1.000	1.197	1.153	.935	—
	r.v.	1.000	1.210	1.172	.883	—	r.v.	1.000	1.222	1.178	.944	—
1st and 2nd	358	24036	27004	27186	23131	101357	356	23780	27807	27163	23586	102336
	Avg.	67.14	75.43	75.94	64.61	283.12	Avg.	66.80	78.11	76.30	66.25	287.46
	r.v.*	1.000	1.123	1.131	.962	—	r.v.*	1.000	1.169	1.142	.992	—
	r.v.	1.000	1.115	1.129	.956	—	r.v.	1.000	1.151	1.146	.997	—
1st, 2nd, and 3rd	358	31257	34826	35647	31404	133134	356	30641	34495	35015	31690	131841
	Avg.	87.31	97.28	99.57	87.72	371.88	Avg.	86.07	96.90	98.36	89.02	370.34
	r.v.*	1.000	1.114	1.140	1.005	—	r.v.*	1.000	1.126	1.143	1.034	—
	r.v.	1.000	1.108	1.138	1.001	—	r.v.	1.000	1.128	1.146	1.037	—

** Four cultures of each of the control and X-ray series excluded because they had fewer than 10 CyL/Pm flies or fewer than 40 flies in all.

in spite of the larger number of CyL/Pm flies hatching in this count in the X-ray series. In both the X-ray and control series there is an indication that the wild-type flies have retarded developmental rates; that is, their ratios to CyL/Pm are lower in the early counts than in the total. This is not unexpected since these individuals are homozygous for their entire second chromosomes which are undoubtedly subvital. It does seem clear, on the other hand, that the wild-type flies of the X-ray series, heterozygous for newly induced changes, have had their developmental rates accelerated; the difference between the ratios of wild-type flies in the two series becomes progressively smaller as the counts accumulate. Hence, the heterotic effect of new mutations includes developmental rates as well as, possibly, differential survival of individuals.

Relation between relative viabilities and culture size. In spite of the similarity of the arrays of culture sizes for the control and X-ray series of test cultures, it seemed worthwhile to determine whether there was a systematic relationship between the relative proportions of flies of different genotypes and culture size. A relationship of this sort, if it existed, could be detected by calculating the regressions of viability on culture size for each person's portion of every experiment

TABLE 8. *A partial analysis of variance of the regressions of relative viability on culture size calculated for each of the 96 entries of table 2.* m.s., F, and p are the same as in table 4.

	CyL/+			Pm/+			+/+		
	m.s.	F	p	m.s.	F	p	m.s.	F	p
Treatment	.000004089	4.55	<5%	.000001424	1.55	—	.000006525	5.34	<5%
Chromosome	.000004836	5.39	<1%	.000002026	2.21	—	.000001724	1.41	—
Assistant	.000001516	1.69	—	.000001627	1.77	—	.000000042	0.03	—
Treat.-chromo. interaction	.000000745	0.83	—	.000000240	0.26	—	.000000145	0.12	—
Treat.-asst. interaction	.000000024	0.27	—	.000001162	1.27	—	.000001841	1.51	—
Chromo.-asst. interaction	.000001613	1.80	—	.000001154	1.26	—	.000000419	0.34	—
Error (residue)	.000000898	—	—	.000000918	—	—	.000001222	—	—

and by testing the significance of the mean of these regressions. If the regressions of relative viability on culture size were significantly different between the two series, it would have to be determined whether this difference alone could account for the observed differences in proportions of CyL/+ and +/+ flies of the two series.

Table 8 represents the results of a partial analysis of variance of these regressions. A single datum for this analysis is the regression calculated for one person's control or X-ray cultures for one experiment; consequently, there are a total of 96 observations (2 treatments × 4 assistants × 12 experiments) or 95 degrees of freedom. These degrees of freedom have been apportioned between treatments, chromosomes, assistants, and the first-order interactions treatment-chromosome, treatment-assistant, and chromosome-assistant. No effort has been made to calculate second-order interactions nor to analyze replicated experiments within chromosomes.

The information presented in table 8 indicates that as far as Plum flies are concerned, there are no significant differences among these regressions associated with any of the factors included in the analysis. In the case of the wild-type and Curly Lobe flies, however, the regressions of relative viability on culture size differ between the X-ray and control series while for Curly Lobe flies these regressions differ for different chromosomes as well. Table 9 lists the mean regressions for all three classes of flies so that the magnitude of the differences may be appreciated. For each of the three classes of flies, the regressions of relative viability on culture size are positive for the control series and negative for the cultures of the X-ray series. These regressions indicate that the gain or loss of a single fly in the size of a culture may have an effect on the observed relative viabilities amounting to several hundredths of one percent.

TABLE 9. *Mean regressions of relative viability on culture size calculated from each of the 96 entries of table 2 and averaged through control and X-ray cultures*

	CyL/+	Pm/+	+/+
Control	0.000133	0.000138	0.000365
X-ray	−0.000280	−0.000105	−0.000156

More detailed analyses of the possible role of these regressions on the calculated viabilities have been made on two bases. In the first of these the significance of the difference between the X-ray and control regressions is ignored and the data on relative viabilities are adjusted by an analysis of covariance (see Snedecor, 1946; p. 320). The cross-products necessary for performing this analysis are listed in table 10. Actually, the covariance analysis has no effect on the significance (or lack of significance in the case of the Plum flies) associated with treatment. Covariance analyses have not been applied to effects other than treatment but this may easily be done by the use of information given in tables 4 and 10.

A second analysis was based on the assumption that the regressions listed in table 9 do indeed differ significantly and cannot be ignored. Limiting our attention to the X-ray and control cultures counted by one person in one experiment, we can ask what would have been the difference in the observed relative viabilities (1) if the true regressions of viability on culture size in the two series were precisely those observed and (2) if the mean number of flies per culture in each series equaled the mean for the two series combined. Under these conditions it develops that the required adjustment of the observed difference in the relative viabilities of the two series is $\frac{1}{2}(b_c + b_x)(\bar{x}_c - \bar{x}_x)$, where b is the slope of the regression, $\bar{x}$ is the mean culture size, and the subscripts c and x refer to control and X-ray cultures. Calculating this adjustment for each of the 48 sets of cultures (4 assistants times 12 experiments) yields mean

TABLE 10. *Summary of crossproducts of relative viabilities and culture size tabulated so that, with the information listed in table 4, analyses of covariance can be made*

Sources of error	d.f.	CyL/+	Pm/+	+/+
Main effects:				
Treatment	1	+ 0.6874	− 0.2985	+ 0.8107
Assistant	3	− 72.0126	+222.0188	+ 86.9506
Chromosome	3	+662.7323	+670.8162	+ 263.7402
Exp. in chr.	8	+350.1375	+238.5670	+ 326.0726
1st order interactions:				
Treat.-asst.	3	− 5.6710	− 8.1490	− 13.9861
Treat.-chr.	3	+ 8.2314	− 5.0114	− 18.2741
Treat.-exp. in chr.	8	+ 54.3120	+ 49.6393	+ 68.1120
Asst.-chr.	9	− 82.9646	− 31.2207	+ 26.2496
Asst.-exp. in chr.	24	− 23.6267	−171.9597	− 44.8323
2nd order interactions:				
Treat.-asst.-chr.	9	− 14.3154	+ 20.2545	− 10.3736
Treat.-asst.-exp. in chr.	24	+103.4259	+ 87.6135	+ 19.1130
Error	1434	+ 99.9628	+420.3871	+1000.7024

adjustments whose absolute values are .001, .0004, and .002 for CyL/+, Pm/+ and +/+ flies, respectively. Needless to say, these adjustments do not differ significantly from zero.

It would appear, then that although some sort of relationship may exist between relative viability and culture size, this relationship does not account for the apparent increase in viability accompanying heterozygosis for newly induced mutations.

Gametic ratios of Pm/(+) and Pm/+ males. The data summarized in table 2 indicate that classes of flies obtaining an irradiated second chromosome from Pm/(+) F_2 males are observed in greater relative proportions than flies of similar genotypes which receive unirradiated wild chromosomes from Pm/+ F_2 males. A possible explanation for this observation lies in distortions of gametic ratios or in proportions of functional sperm produced by the parental males rather than in the differential viability of developing larvae.

This possibility has been tested by counting the offspring produced by single pair matings of Pm/+ and Pm/(+) males (brothers of the parental males of the F_3 cultures of experiment #6) and Ore-R females in half-pint culture bottles. To insure that these cultures would not be over-crowded, the parental pairs were allowed to remain only four days. The offspring were counted last on the 17th day.

The results of this test can be summarized briefly as follows: Of 8573 offspring obtained from 36 Pm/(+) males, 49.8% were wild-type; of 6772 offspring produced by 35 Pm/+ males, 50.9% were wild-type. The results of the two series of matings do not differ significantly from one another nor does either indicate that these Plum flies are producing gametes in any other than the expected 50–50 ratio. Consequently, there is no indication that the results of our experiments are to be explained by disturbances of gametic ratios.

Background chromosomes. Before making the statistical analyses of the proportions of flies of different genotypes at various times during the hatching of the F_3 cultures, a separate test for possible effects of irradiated background chromosomes had been made. This test con-

sisted of mating Pm/+ flies hatching in the F_3 cultures of both the X-ray and control cultures with CyL/Pm virgin females. As far as their second chromosomes are concerned, these Pm/+ flies were identical for even in the X-ray series the non-Plum second chromosomes of these flies is a non-irradiated chromosome. These males do differ, however, in that about one quarter of those coming from the F_3 cultures of the X-ray series are heterozygous for an irradiated third chromosome (and another quarter heterozygous for an irradiated fourth). In mating these flies with CyL/Pm females one expects to recover three classes of flies—CyL/Pm, CyL/+, and Pm/+—in approximately equal proportions. The offspring of the Pm/+ males of the X-ray series will carry irradiated third and fourth chromosomes much as the four classes of flies of the F_3 X-ray cultures do. Because this test introduced one more generation of "dilution," the Pm/+ males used were chosen from a different set of experiments; they were taken from the F_3 cultures of an experiment (7-F) in which the original irradiated wild-type flies were females exposed to 1000r. It was hoped that the greater initial exposure would at least partially compensate for the further dilution of irradiated background chromosomes.

The data obtained from 40 X-ray and 40 control cultures of this test gave no indication that the irradiated third and fourth chromosomes were affecting our observed results. As before, the CyL/Pm flies were used as the standard for measuring viability. The relative viabilities of CyL/+ and Pm/+ flies in the control series were 1.073 and 1.273 respectively; the same classes in the X-ray series of cultures had relative viabilities of 1.069 and 1.292. These differences are not significant. They offer no assistance in explaining the results listed in table 2; in fact, taken at face value the results of this test are the reverse of those required as an explanation.

Non-disjunction and the suppression of the Plum phenotype. A possible source of error in the type of experiment described in this paper arises from the fact that the Plum phenotype is suppressed by the presence of an extra Y-chromosome in either sex and Pm/+ flies may be classified as wild-type. This was not expected to present serious difficulties since the irradiation was given to mature sperm which already possessed their complements of chromosomes and since the parental females of the F_3 cultures were sibs. Nevertheless, the results of the test described in the preceding paragraph shed some light on the frequency of non-disjunction and these data will be reported here.

The offspring expected from crossing Pm/+ males and CyL/Pm females consist of three genotypes—CyL/Pm, CyL/+, and Pm/+; wild-type offspring are not expected. However, a few flies hatched in the 80 cultures which phenotypically had to be considered wild-type. These were all females. Among the 40 X-ray cultures, there were eleven of these females in addition to 6245 Plum flies of both sexes; among the 40 control cultures there were eight in addition to 6371 Plum flies. By mating these females with white eyed males it was possible to show (1) that in spite of their wild-type phenotype they carried Pm chromosomes and (2) that they possessed Y-chromosomes since occasional white eyed sons appeared among the offspring of these crosses.

These phenotypically normal females were distributed randomly among the 80 cultures; 63 cultures had none, 15 had one each, and two cultures had two exceptional females. In each case where two of these normal females occurred in the same culture bottle, they hatched on different days.

Mis-classification of flies. A final test in our search for an explanation other than heterosis in explaining the results shown in table 2 concerned the possibil-

ity that systematic errors were occurring in the classification of flies in the F_3 cultures. In counting a large number of flies, occasional errors in classification are to be expected; indeed, if the data are sufficiently extensive one expects eventually to detect significant differences between persons in this respect. These accidental mistakes are not important in the present type of investigations, unless, for unknown reasons, they are not randomly distributed between the X-ray and control cultures. In looking for the possible presence of systematic errors in classification, the tests were restricted to wild-type males hatching in the F_3 cultures. The use of wild-type males was based on the fact that flies classified as mutants are those which show the mutant phenotype while "wild-type" flies are really a residue consisting of nonmutant individuals and mutant individuals whose phenotypes are not expressed.

The first test for misclassification was made under near-emergency conditions during the 6th experiment. Because of exceptionally cold weather, the circulation of air in the constant temperature room was inadequate to maintain the usual temperature of 25°. In making the last counts it became apparent that the classification of flies had become especially difficult. A supply of CyL/Pm virgins was available, so a sample of presumed "wild-type" males was mated in order to ascertain their actual genotypes. If a tested male were really wild-type, only CyL/+ and Pm/+ offspring would be obtained; if, however, the tested male were CyL/+ or Pm/+, there would be CyL/Pm offspring as well. Although the test does not distinguish between CyL/+ and Pm/+ males, the former are much more likely to be included among the normal individuals; Curly wings tend to be straight when flies develop at low temperatures and small flies from crowded cultures sometimes have poorly expressed Lobe phenotypes.

Eighty-four males from the control cultures were tested at this time and 15 of these proved to be non-wildtype; 109 males of the X-ray series were tested and of these 7 were non-wildtype. The difference between the two series is significant (Chi-square of 5.2, one degree of freedom, probability of .02).

This high frequency of misclassification is disturbing but it must be remembered that the test was made for the experiment in which it was obvious that classification had become difficult. Since the difficulty in classifying flies arose in the last count, and since somewhat less 25% of the flies hatching in these cultures occurred in this count, the error for the experiment is undoubtedly much smaller than the tests themselves indicate. Furthermore, it will be noted that the results indicate that this type of error *increases* the relative proportion of wild-type flies in the control more than in the X-ray series probably at the expense of the CyL/+ flies. Consequently, although these results might help explain why the CyL/(+) flies of the X-ray series seem to have higher viabilities than those of the control, they offer no explanation for the differences between the relative viabilities of the wild-type flies of the two series.

To test whether the high proportion of misclassified flies was indeed unique to the period of abnormally low temperatures, the test of wild males was repeated during experiment 9. At this time Ore-R virgins were available so that misclassified flies could be identified as to proper genotype. However, of 235 flies from the X-ray cultures and 229 males from the control cultures, none was misclassified. These results indicate that the errors in classification in the earlier experiment (#6) were most likely unique to that experiment. However, the fact that misclassifications differed in frequency between the X-ray and control cultures suggests that systematic errors can occur but, in the present experiments, these are apparently unable to explain the relatively high frequency of wild-type flies

heterozygous for irradiated chromosomes since the bias was in the opposite direction.

Summary. The experimental results presented in table 2 indicate that flies carrying two second chromosomes identical except for random changes induced by the exposure of one member of the pair to 500r X-radiation have mean viabilities exceeding individuals homozygous for an unirradiated pair of identical chromosomes. A number of tests for factors other than heterosis that could duplicate the observed results have either yielded negative results or have revealed phenomena whose small effects are unlikely to be responsible for the apparent heterotic effect.

Subsequent, incompletely analyzed experiments. The type of study reported here has been continued with modifications in the mating scheme and in experimental techniques. The results of these experiments have not been analyzed as fully as those described above, but a summary of the results obtained so far may be of some interest in the present context.

While adhering to the general procedures indicated in figure 2 it has been possible (1) to initiate experiments with homozygous wild-type females exposed to 1000r rather than with males exposed to 500r as described above, (2) to initiate other experiments with homozygous females exposed to 500r, (3) to manipulate the final mating so that the Curly Lobe flies of both the X-ray and control F_3 cultures carry non-irradiated wild chromosomes while the Plum flies of the X-ray series do carry exposed chromosomes, and (4) to introduce irradiated background chromosomes into the control cultures by initiating the control series with irradiated CyL/Pm males mated to non-irradiated wild-type females.

Each of these sets of experiments has consisted of analyzing 600 or more control and an equal number of X-ray cultures. The observed differences in viability have not been significant in the case of each set of experiments but the results have been consistent so that the results become significant when the data are consolidated: In five experiments involving over 7000 cultures in which the Plum flies of the X-ray and control series are supposed not to differ, the probability that the small observed difference could occur by chance is approximately 70%. In these same experiments, the relative viability of CyL/(+) flies of the X-ray series exceeds that of the CyL/+ flies of the control by an amount that is significant at the 5% level. (There was only one experiment in which the relative viability of the CyL/(+) flies was below that of the CyL/+ individuals of the controls.) Finally, in six large experiments involving some 7600 cultures in which +/+ and +/(+) flies have been compared, the relative viability of the new heterozygotes has consistently exceeded that of the control homozygotes; these results are significant at the 0.2% level. The small difference observed between the control and X-ray series in average number of flies per culture is not significant; the probability that this difference could occur by chance is 60%.

Discussion

In an earlier section two questions were raised: (1) To what extent do Mendelian populations deviate from the complete genetic uniformity expected as the final outcome of selection for "normal" homozygous individuals? (2) What is the reason for this deviation? It is well known that mutation pressure frustrates the attainment of complete homozygosis and, at least in theory, the amount of heterozygosity resulting from this pressure can be calculated rather easily. A quantitative estimate of the extent to which the selective superiority of heterozygotes contributes to the failure of a population to achieve complete homozygosis has not been available. The argument described earlier in this paper and

outlined in figure 1 offers a means for making this estimate.

The failure of earlier work to furnish a basis for estimating proportions of loci at which heterotic alleles exist does not imply that this work has failed to demonstrate the importance of heterosis in maintaining polymorphism, cryptic or otherwise, in populations. Such polymorphic systems have been found in a wide variety of organisms, including man, and the degree to which heterozygotes exceed homozygotes in fitness is occasionally startling. In many instances, especially in cases of chromosomal polymorphism where numerous loci are involved, it is difficult to distinguish between over-dominance and pseudo-overdominance based on dominance-recessive relationships at many linked loci. Robinson and Comstock (1955) have described a situation in maize where segments of chromosomes derived from different inbred strains exhibit an apparent overdominance but this effect dissipates with the advent of gene recombination. Nevertheless, in Drosophila there are indications that F_1-, three-way, and double-cross hybrids differ in their mean viabilities (see, for instance, Wallace and Vetukhiv, 1955); simple dominance does not easily account for these differences. Nor does the simple dominance of "normal" alleles explain the fact that individuals homozygous for "supervital" chromosomes exhibit their supervitality under a very limited range of environmental conditions (Dobzhansky *et al.*, 1955); according to the model of homozygote superiority one would assume that these supervital homozygotes approximate very closely the "ideal" genotype of figure 1.

If one were to limit his attention to the wildtype flies of the experiments described in the present report, our data would indicate that heterosis is a common phenomenon. The increase in mean viability which accompanied irradiation implies that a chromosome obtained from a reasonably large population carries at most gene loci—at 70% or more of all loci-alleles which are somewhat deleterious when homozygous. A high proportion of such "deleterious" alleles is most reasonably explained by the selective superiority of individuals heterozygous for two different forms of such alleles.

A comparison of the relative viabilities of the CyL/+ and CyL/(+) flies of the two series makes the above interpretation somewhat insecure. If most members of a Drosophila population are heterozygous at a majority of all gene loci, one would expect that individuals heterozygous for the CurlyLobe and wildtype chromosomes are also heterozygous for alleles at most gene loci. Obviously, a mutation which is induced in the wildtype chromosome at a locus for which CyL/+ flies are already heterozygous will not increase the proportion of heterozygous loci; only mutations at those—presumably infrequent—loci which are occupied by the same allele in both the CurlyLobe and wildtype chromosomes effectively increase the proportion of heterozygosity. According to our argument, the latter mutations alone are expected to result in an occasional improvement in viability; randomly induced mutant alleles are not expected to be heterotic more often than preexisting alleles which are already present in the heterozygous condition.

A firm decision regarding the two proposed models cannot be made at the present time on the basis of the data presented in detail in this report. This decision must rest (1) on the reality of the observed differences in viabilities of flies carrying irradiated and non-irradiated chromosomes and (2) on the correct interpretation of these differences should they be real. In the case of the wildtype flies, there is little doubt concerning the reality of the difference in relative proportions observed between the x-ray and control cultures; in the case of the CurlyLobe flies, despite the fact that the magnitude of the apparent increase in viability is nearly as large as that of the wildtype

flies, the reality of this difference is less certain. For the data described in detail, the probabilities that the observed increases in viability of wildtype and CurlyLobe flies are due to chance are 0.02 and 0.04 respectively; for all available data these probabilities are 0.002 and 0.04. The additional information has not changed the level of significance in the case of the CurlyLobe flies while it has lowered that of the wildtype flies considerably.

The viability changes which are under investigation in this type of study are extremely small. This fact has two important consequences: First, small experimental biases which could be ignored in many studies may, in the present type of experiment, lead to a mis-interpretation of the results. This is the reason why experimental techniques and supplementary tests were described in detail; no errors of this sort have been revealed by these tests. Second, the smallness of the radiation effects makes it virtually meaningless to ask whether the increase in viability observed for wildtype flies is larger than that observed for CurlyLobe flies. The experimental error accompanying the comparison of increases in viability for the two classes of flies is considerably larger than the error by means of which the x-ray series of either class is compared with its own control. Because mean differences are small, any analysis of these data which results in an increase in error variance will almost certainly fail to give significant results.

In summary, we conclude that the experimental results described above are consistent with and offer strong support for the model of population structure which is based on the selective superiority of heterozygous individuals; they offer no support whatsoever for the alternative model. At the same time, it must be pointed out that this conclusion rests on the assumption that further analyses of available data and additional experimental tests will furnish a satisfactory explanation for the apparent viability difference between CyL/+ and CyL/(+) individuals.

Summary

The work reported here represents a preliminary attempt to obtain experimental data that will allow one to estimate the proportion of loci for which an individual of a diploid and normally outbred species (such as Drosophila) is heterozygous. The argument proceeds as follows: If a population contains primarily normal, wild-type alleles at each locus with the exception of deleterious alleles arising through mutation, then homozygous individuals obtained artificially by genetic techniques would differ at very few loci from the normal individuals found in the population itself. Consequently, an overwhelmingly large proportion of random mutations would be expected to lower the viability of these homozygous individuals even if these mutations were tested in the heterozygous condition. Any evidence that a substantial proportion of random mutations increases the viability of these homozygotes demands a corresponding modification of the concept of essential homozygosis of individuals comprising the population.

Using second chromosomes obtained from an experimental population of *D. melanogaster* and techniques illustrated in figure 2, evidence has been obtained which indicates that newly induced mutations tested in the heterozygous condition increase the average viability of otherwise homozygous individuals.

On the basis of our results we have tentatively concluded that on the average an individual member of the Drosophila population studied is heterozygous for genes at 50% or more of all loci; that is, more than half of the alleles actually present in a given chromosome were seemingly improved by heterozygosity for a randomly induced allele. The tentative nature of this conclusion is demanded by the apparent—but much less certain—in-

crease in viability exhibited by Curly Lobe flies heterozygous for irradiated wildtype chromosomes. Furthermore, this estimate does not attempt to evaluate the importance of those factors which limit heterozygosity within populations or, in the case of inbreeding and chance, actively promote homozygosis.

Acknowledgments

The author wishes to acknowledge the assistance of Carol Madden, Jennie Buchanan, Gloria Casillo, Ellen McMullen, and Olga Sokoloff in carrying out these experiments. He wishes to thank, too, Professor Th. Dobzhansky and Dr. J. C. King for extended discussions and Dr. A. E. Brandt for introducing him to the analysis of covariance. Finally, he wishes to express his gratitude to Professor Everett Dempster for many thoughtful criticisms and suggestions which, although not completely followed, were of immense value.

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NOTES AND COMMENTS

300 SPECIES OF DROSOPHILA IN HAWAII?—A CHALLENGE TO GENETICISTS AND EVOLUTIONISTS

ELWOOD C. ZIMMERMAN

British Museum (Natural History), London

Since I became aware, many years ago, of the astonishing development of *Drosophila* in Hawaii, I have tried to interest geneticists and evolutionists in the fauna, but I fear that it has been considered, at least by some workers, that my descriptions of the size and diversity of the fauna are exaggerated. I do not exaggerate; the fauna is extraordinary! It is possible that the Hawaiian drosophilid fauna may be the most remarkable in the world. In Hawaii is found a range from unusually small species to absolute giants up to about a centimeter across, and there is much morphological diversity. There may be as many as 300 species concentrated in an area smaller than the little state of Massachusetts or less than one-fifth the size of Ireland. Where else has such a drosophilid fauna developed? Is this fauna not worthy of detailed attention by those equipped to do advanced research on the genetics and evolution of this group of fascinating flies?

A number of years ago, when I was actively working in Hawaii, I tried to interest the late Prof. Richard Goldschmidt in the fauna. He replied that he had been scheduled to go to Hawaii for study, but the outbreak of the first world war prevented his going. Then, unhappily, the second world war thwarted the attempt of one of his students to go to Hawaii to study the *Drosophila*. What an unfortunate thing it is that neither man was able to carry out his plan. With the extensive background of knowledge of *Drosophila* amassed in recent years, the time is now even riper for an advanced attack on the Hawaiian drosophilids.

Why should so many species of *Drosophila* have evolved "explosively" in Hawaii? What is the driving force behind such evolution in these isolated islands? Why should there be more species in these geologically young, volcanic, oceanic islands than in the entire United States which is about 500 times larger in area and is infinitely older and ecologically much more diversified? We know comparatively little of the ecology of any of the Hawaiian species. How do they fit into the environment and how do so many species exist in such close proximity? What are their patterns of distribution? What are their food requirements? What? Why? How?

R. C. L. Perkins, as long ago as 1913, in his classic "Introduction" to "Fauna Hawaiiensis" (Cambridge Univ. Press, p. clxxxix) said that in Hawaii ". . . *Drosophila* is represented by an assemblage of species, exhibiting great diversity in structure and appearance. . . . At present these insects, many of which are obscure and minute forms, have been very imperfectly collected. To make an approximately complete collection and thorough study of the Hawaiian species would require the devotion of many years of special work. Not less than 250 species must exist in the islands, and double that number may very probably occur." Perkins had difficulty preserving delicate Diptera under the trying conditions he had to endure when he originally explored the islands before the turn of the century, and he did not make a special effort to amass a large and comprehensive collection of the Hawaiian flies. Certainly, he did not collect flies as completely as he did some of the other major orders of insects. It is most unfortunate that extensive collections of *Drosophila* were not made in Hawaii many years ago, because the native drosophilids have now been exterminated over vast areas of the islands, because of the activities of man and the predators and parasites he has introduced. The area now occupied by native species is much less than one-half of what it once was. We do not know and can never know what the lowland faùna was.

We know now that Perkins was correct when he said that "not less than 250 species" must occur in Hawaii. Dr. D. Elmo Hardy, University of Hawaii, is now writing the volumes on the Diptera for my series "Insects of Hawaii" (University of Hawaii Press, Honolulu). The drosophilids from the various collections in Hawaii have been assembled, and Hardy has done considerable recent collecting himself. He already has before him about 200 species of *Drosophila,* and he will report upon these in his forthcoming volume on the Hawaiian Drosophilidae (it will take a large, complete volume of "Insects of Hawaii" just to report upon the

Hawaiian species from what some people now like to refer to as the "alpha" level of systematics). In spite of the large size of Hardy's report on the drosophilids, only a fraction of the area of the Hawaiian Islands has yet been explored, even superficially, for *Drosophila*. When Hardy's book is published, geneticists and evolutionists will have a foundation to guide them in advanced and specialized studies of the Hawaiian *Drosophila*.

As a student of some years experience in island faunas, I wish to urge those who are equipped to do specialized research on *Drosophila* to look to the Hawaiian drosophilid fauna as a veritable mine of possibilities for exciting and profitable study.

MORPHOLOGICAL INTEGRATION [1]

JOHN IMBRIE

Columbia University, New York

The Euclidian dictum that the whole is equal to the sum of its parts is true of organisms only in a trivial sense. Nevertheless, for purposes of focusing attention on one aspect of an evolutionary or taxonomic relationship, analysis into individual anatomical parts and dimensions is a necessary first step in most biological studies. To arrive at a satisfactory synthesis following such a dissection, anatomical elements must not only be articulated, but scrutinized for dynamic and functional interrelationships as well. What Olson and Miller have done in this book is to present both a rational fundation and a statistical methodology for achieving such a synthesis. Although the approach is new, their point of view may be expressed by T. H. Huxley's epigram: The constituents of animal bodies are not mere unconnected parts, but organs working together to an end.

In essence the authors' method is to calculate a correlation coefficient (r) between all possible pairs of a selected number of anatomical measurements in a given sample and scan the resulting array of coefficients for strongly intercorrelated groups of measures. Empirical and theoretical grounds are presented for the belief that a group so formed (designated a *ρ-group*) is the statistical reflection of an underlying functional or developmental relationship. Thus in any given study the primary objective is to discover and document the existence of ρ-groups. With this done, a variety of secondary treatments can be applied. Partial correlation, for example, can be used to assess and remove the influence of gross size (or of other agents) on the total correlation; and the overall intensity of integration in the total array of measurements can be recorded by a newly developed *index of morphological integration*.

With obvious limitations of experimental design and operator error, this method shares with other biometric techniques the inherent merits of objectivity, reproducibility, and accuracy of expression. The critical reader will nevertheless pose the question: Could results be gained by simpler means? In the reviewer's opinion, the class of relationships treated in this book cannot in any really satisfactory way be handled intuitively or by any non-quantitative method. Photographic documentation is impossible, and verbal description would usually serve to obfuscate rather than clarify the inquiry. Statistical procedures of the sort exemplified in this study justify themselves primarily because they provide a means of reducing subtle and abstract relationships to concrete terms.

Before discussing Olson and Miller's work further it may be helpful to cite briefly some of their actual results:

1. Two experiments (with the squirrel *Sciurus* and the frog *Rana*) are described in which samples drawn from living populations are used to justify the assumption that ρ-groups derived statistically from osteological measurements correspond to functionally related groups of anatomical elements.

2. Use of the index of integration on various ontogenetic stages of the albino rat reveal phases of strengthening and weakening of the intensity of total morphological integration.

3. Data on the Mississippian blastoid *Pentremites* show that an increase in the level of morphological integration is recorded just after the splitting of a parent stock into two descendent lines. This is followed by a marked decrease.

4. Similar data on the Eocene condylarth *Hyopsodus* show a different pattern characterized by a gradual decrease in the level of integration in each of two phyletic lines.

5. Examination of stratigraphically ordered *Hyopsodus* samples, assigned by classical mor-

[1] By Everett C. Olson and Robert L. Miller. The University of Chicago Press, 1958. 317 pp., 81 figs., 111 tables. $10.00.

phological analysis to two stocks displaying parallel features of dental evolution, reveals that the patterns of morphological *integration* are divergent rather than parallel. The parallelism is interpreted as the acquisition of dental features more effective for the herbivorous life in general, as opposed to the divergent integration pattern which is taken to reflect a functional adaption to varied herbivorous diets.

Viewed strictly as contributions to the knowledge of morphogeny and evolution of the albino rat, *Pentremites,* and *Hyopsodus,* these achievements clearly do not justify the labor involved. The real significance of Olson and Miller's work lies in quite another, more broadly significant, field of inquiry: the behavior of morphological integration in evolution. Here they have provided a framework within which questions pertinent to the topic of evolution as a whole can be asked and answered. Does the intensity of morphological integration tend to increase as more complex forms evolve? What is the role of integration in speciation? Does integration evolve? These and other questions are posed by the authors. Although the few answers they attempt are tentative and necessarily based on incomplete evidence, this should not detract from the importance of their overall contribution.

Clearly this is not a book for the general reader. The method as here expounded should, however, be intelligible to any student with a degree of statistical sophistication that includes a grasp of partial correlation and the basic principles of statistical inference. In many places the writing is definitely abstruse, although to what extent this is due to the authors' style and to what extent to the inherent subtlety of the subject matter is not clear. In any case this difficulty is compounded by numerous small but annoying errors in the captions and body of many tables and figures. Another shortcoming of the book is the lack of a clear, step-by-step introduction into the actual techniques that would enable a potential user of the method to begin calculations on his own. The entire analysis, for example, hangs on the computation of a large number of total and partial correlation coefficients, a task that is essentially impossible without the aid of electronic data processing devices. At least a brief statement of these procedures should have been included.

REPORT ON THE THIRTEENTH ANNUAL MEETING OF THE SOCIETY FOR THE STUDY OF EVOLUTION

HARLAN LEWIS

The Thirteenth Annual Meeting of the Society was held at the University of Michigan, August 31–September 3, 1958, in conjunction with the annual meeting of the Society of Vertebrate Paleontology. Total registration was 173, including 60 from Michigan, 16 from Illinois, 14 from California, and 11 from New York. United States registrants came from 26 states and the District of Columbia. In addition, a number of members came from Canada, two from Italy, and one from Germany. The Local Committee responsible for the excellent arrangements included Warren H. Wagner, Jr., Chairman, Emmet T. Hooper, Erich E. Steiner, and Robert W. Storer.

MINUTES OF THE BUSINESS MEETING, SEPTEMBER 2, 1958

The meeting was called to order at 4:30 P.M. by President Colbert.

1. The minutes of the last business meeting, Stanford University, September 25, 1957, were approved as read.

2. The Secretary announced the officers and councilmen elected for 1959:
President, Edgar Anderson
Vice Presidents, Harlan Lewis, J. W. Gregor, N. Tinbergen
Secretary, Herbert H. Ross
Editor, I. Michael Lerner
Councilmen, W. Frank Blair, Jens Clausen

3. The Editor presented his final report on the status of EVOLUTION, indicating that it is a flourishing international journal. He also pointed out that, because of increases in the expense of publication, EVOLUTION has run a budget deficit for the past three years.

4. The Treasurer summarized his report for the year ending December 31, 1957. This report indicated an operating deficit of about $350 for the year. In his interim report, he indicated that a comparable deficit can be expected for 1958. He also reported a contribution of $583.41 from 240 individuals to the fund for travel grants to enable overseas geneticists to attend the Genetics Congress in Montreal.

5. The Secretary summarized the reports received and the action taken at the Council Meeting on August 31, 1958.

a. The Secretary has received the final report of the Committee on Evolution and Behavior—a joint committee of the Society for the Study of Evolution and the American Psychological Society. The results of the activities of the committee are being published in a Symposial Volume by Yale University Press. The Society holds a contract with the Press whereby profits from the volume will be shared equally by the two sponsoring societies.

b. The following Associate Editors were appointed for a three year term: Raymond B. Cowles, Los Angeles; R. A. Stirton, Berkeley; Reed C. Rollins, Cambridge, Mass.; D. B. O. Savile, Ottawa; Antonio Brito daCunha, Sao Paulo; Pavel V. Terentjev, Leningrad.

c. An invitation from the Society of Systematic Zoology to cosponsor the program they have arranged as a Bicentennial Celebration of the publication of Linnaeus' 10th Edition of *Systema Naturae* was accepted. The program will be held with the A.A.A.S. at Washington, D. C. in December, 1958.

d. The Annual Meeting in 1959 will be held at the University of Chicago in November in conjunction with the Darwin Centennial Celebration arranged by the University of Chicago. Everett C. Olson is chairman of the local committee.

e. A committee was appointed by the President to study the problem of the increasing demand on the time of the officers, particularly the Treasurer who is also Business Manager for EVOLUTION.

f. A budget of $10,000 for publication of EVOLUTION in 1959 was approved.

g. The Council decided to increase the price of back volumes of EVOLUTION to $6 for members and $7 for non-members, effective October 1, 1958.

h. After a discussion of the financial status of the Society, including the deficit of 1957 and the anticipated deficit for 1958, the Council decided to recommend to the members of the Society that annual dues be increased to $6 (effective for 1959) and that subscriptions be increased to $7.

6. The Secretary presented a motion on behalf of the Council to amend By-laws, Article 1, DUES, first sentence, by changing $5.00 to $6.00. The sentence as amended to read "The annual dues of members shall be $6.00, including subscription to the journal." The motion passed unanimously.

7. The Secretary presented a motion on behalf of the Council to amend By-laws, Article 2, PUBLICATIONS, by deleting the second sentence, which reads "The membership dues are $5.00 yearly, of which $4.00 is subscription for the journal.", and by changing $6.00 in the third sentence to read $7.00. The first para-

graph of Article 2 as amended to read: "The Society shall publish a journal in the field of evolution and such other publications as authorized by the Council. Non-members and institutions may subscribe to the journal at the rate of $7.00 per volume." In the discussion it was pointed out that in 1957 the publication cost of EVOLUTION was $5.10 for each copy of that volume. The motion was passed unanimously.

8. A motion of appreciation for the work of the Local Committee was approved by acclamation.

The meeting adjourned at 5:15 P.M.

PROGRAM

The program of papers included the Presidential Address, a public lecture, two symposia, demonstrations in the local laboratories, and contributed papers.

Presidential Address: Evolution and Extinction, EDWIN H. COLBERT, American Museum of Natural History.

Public Lecture: Evolution before Darwin, MARSTON BATES, University Michigan.

Symposium: Darwin's Impact on Modern Biology, arranged by President Colbert.

JENS C. CLAUSEN, Carnegie Institution of Washington. Variation and Cohesion as Evolutionary Principles.

JOHN A. MOORE, Columbia University. Populations and Natural Selection.

W. FRANK BLAIR, The University of Texas. Behavior and Hybridization.

JAMES F. CROW, The University of Wisconsin. Genetics and the Origin of Life.

HORACE E. WOOD, 2ND, Rutgers University and the American Museum of Natural History. The Geologic Record and the Stratigraphic Succession.

JAMES A. OLIVER, New York Zoological Park. Geographical Distribution.

ALFRED S. ROMER, Harvard University. Phylogeny and Morphology.

Symposium: Problems of Vertebrate Phylogeny, arranged by the Society of Vertebrate Paleontology.

ROBERT H. DENISON. Relationships of the Placoderms and Acanthodians.

BOBB SCHAEFFER. Aspects of Actinopterygian Phylogeny.

FRANK PEABODY. The Primary Branching of the Reptilia (Posthumously presented by Theodore Eaton).

RAINER ZANGERL. Triassic Squamata.

EVERETT C. OLSON. Therapsid Ancestors of the Mammalia.

ALAN BOYDEN and ELIZABETH O. PAULSEN. Serology as an Aid to Systematics.

SAMUEL B. MCDOWELL. Anatomical Basis for Insectivore Classification.

MALCOLM C. MCKENNA. New Data on Insectivore Relationships.

ALBERT E. WOOD. Fossil Evidence of Rodent Phylogeny.

Contributed Papers and Demonstrations:

ALEXANDER, RICHARD D., University of Michigan. The Evolution of Tegminal Stridulation in the Ensifera (Orthoptera).

ARMSTRONG, J. T., University of Michigan. Effects of Food and Immigration on Flatworm Populations (Demonstration).

BLASDELL, ROBERT F., Polyploidy in the Fern Genus *Cystopteris* (Demonstration).

BROWN, WILLIAM L., JR., Harvard University. The Kinds of Adaptation.

CARPENTER, JOHN M., University of Kentucky. Studies on the Causes of Fluctuations in *Drosophila* Species.

EMERSON, ALFRED E., University of Chicago. Regressive Evolution in Termites.

EPLING, CARL, University of California, Los Angeles. A Static of Evolution.

EVANS, FRANCIS C., and M. FOSTER, University of Michigan. The Work of the Mouse Genetics Laboratory (Demonstration).

HAIRSTON, NELSON G., University of Michigan. Competition and Community Structure.

HAPP, GEORGE B., The Principia College. An Emerging Synthesis in Evolution.

HIRAIZUMI Y., L. SANDLER, and J. F. CROW, University of Wisconsin. An Example of Meiotic Drive in a *Drosophila* Population.

HOTTON, NICHOLAS, III, University of Kansas. Position of Tympanum in Pelycosaurs and Its Evolutionary Significance.

HUBBS, CLARK, University of Texas. Duration of Sperm Function as a Factor in Frequency of Fish Hybridization.

JOLLIE, MALCOLM T., University of Pittsburgh. The Phylogeny of the Falconiforms (Hawks).

LEWIS, HARLAN, University of California, Los Angeles. Evolution of Synthetic Populations of *Clarkia* in Natural Habitats.

LITTLEJOHN, MURRAY J., University of Texas. Evolution in the Australian Genus *Crinia* (Anura, Leptodactylidae).

LOWRY, ROBERT J., University of Michigan. The Chromosomes of Basidiomycetes (Demonstration).

LUDWIG, WILHELM, University of Heidelberg. The Evolution (Acquisition) of *Least* Heritable Dextro-sinistral Differences in Dual Organs of Insects, Interpreted by Geoffroyism.

MATTONI, R. H. T., University of California, Los Angeles. Lethals and the Genetic Structure of Some Populations of *Drosophila pseudoobscura*.

MILLER, ROBERT R., University of Michigan.

Unisexual Vertebrates—A Review of Known Cases.

MILLER, ROBERT R., and R. J. SCHULTZ, University of Michigan. The Biosystematics of a Genus of Viviparous Fishes (Demonstration).

MOORE, T. E., and R. D. ALEXANDER, University of Michigan. The Use of Insect Sounds in Systematics (Demonstration).

RUIBAL, RODOLFO, University of California, Riverside. Ecological Analysis of a Desert Population of *Rana pipiens*.

SAVAGE, JAY M., University of Southern California. Problems in the Evolution of Lizards.

SLOBODKIN, L. B., University of Michigan. Effects of Food Availability and Predation on Population Dynamics of Hydra (Demonstration).

STARRETT, ANDREW, University of Southern California. Insular Evolution in the Meadow Mouse in Massachusetts.

STEINER, ERICH E., University of Michigan. Research on the Genetics of *Oenothera* (Demonstration).

VAN DER SCHALIE, HENRY, University of Michigan. Studies of Systematic Relationships of Six Species of Amphibious Snails (Demonstration).

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